

LEARNING TO OVERCOME THE BINDING PROBLEM

by

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Abstract

The work presented in this thesis considered the binding problem; how segregated visual information becomes unified and our perception coherent. This thesis is divided into two parts, each focused on proposed binding solutions.

Part 1 examined the binding processes that parse information at early stages of visual processing, perhaps prior to the engagement of attention. These grouping processes were examined in visual extinction patients, as an assay of pre-attentive processing. I demonstrated that item similarity can exacerbate as well as alleviate extinction, depending on the display conditions. Exacerbation of spatial deficits was shown when the array parameters encourage stimuli to be processed as distinct elements (Chapter 2). Where displays promote grouping of items both spatial (Chapter 2) and temporal (Chapter 3) impairments in extinction may be overcome.

Part 2 considered the effects of learned associations on feature binding. I focused specifically on the processing of objects with an associated, so called ‘diagnostic’, colour. I demonstrated that for such stimuli, binding of these features is automatic (Chapter 4) and modulated performance even to ones determinant. Subsequently I examined how this binding interacts with attention in a series of visual search experiments. I found that, under conditions requiring colour-shape feature conjunction, appropriately coloured targets ‘popped-out’ whereas incorrectly coloured depictions did not (Chapter 5). Converging neuropsychological evidence from visual extinction suggested that binding of learned features might not engage serial attentive processes (Chapter 6). Finally, an fMRI study was carried out to examine brain areas sensitive to the congruency of colour-shape associations; binding consistency affects the earliest stage of processing (Chapter 7). I provide evidence for efficient conjunction coding of associated features highlighting learning as one way the brain may overcome the binding problem.

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Table of Contents

<i>CHAPTER 1: GENERAL INTRODUCTION</i>	<i>1</i>
The Binding Problem	1
Binding Solutions	2
Different forms of binding	5
Effects of stored knowledge on binding	7
Colour effects in object recognition	10
Part 1: The effects of item similarity on extinction; when and how is it beneficial?	13
<i>Chapter 2: From helping to hurting:.....</i>	<i>14</i>
<i>Shifting the effects of similarity on visual spatial biases in extinction</i>	<i>14</i>
Synopsis	14
Introduction	15
General Method	19
Experiment 1: Wide separations plus a fixation cross	21
Method	21
Results and Discussion	23
Experiment 2: Small separations plus a fixation cross	26
Method	26
Results and Discussion	26
Experiment 3: Wide separations, no fixation cross	28
Method	28
Results and Discussion	28
Experiment 4: Small separations no fixation cross	30
Method	30
Results and Discussion	30
Across-Experiment Comparison	32
Discussion	33
<i>Chapter 3</i>	<i>36</i>
<i>The grouping benefit in extinction:.....</i>	<i>36</i>
<i>Overcoming the temporal order bias</i>	<i>36</i>
Synopsis	36
Introduction	37
Method	40
Results	44
Discussion	47
Part 2: Binding of learned features	50
<i>Chapter 4</i>	<i>51</i>
<i>Disruptive effects of diagnostic colour at different levels of processing: Evidence for the automatic linkage of colour-shape object representations</i>	<i>51</i>
Synopsis	51
Introduction	52
Experiment 1: Unlimited Exposure	57
Method	57
Results	59
Discussion	61

Experiment 2: Brief stimulus durations	64
Method	64
Results	64
Discussion	67
Experiment 3: Brief presentations with fixated backgrounds	69
Method	71
Results	72
Discussion	74
Experiment 4: Colour Naming	75
Method	75
Results	76
Discussion	76
General Discussion	78
<i>Chapter 5.....</i>	<i>81</i>
<i>Evidence for spatially parallel binding of</i>	<i>learned conjunctive relations.....</i>
Synopsis	81
Introduction	82
Experiment 1a: Three object colours, equally likely	88
Method	88
Results and Discussion	90
Experiment 1b: Three target colours with geometric forms	96
Method	96
Results and Discussion	97
Experiment 1c: Effects with background colours	101
Method	101
Results and Discussion	102
Experiment 2a: Non-Target Colour-Congruency Effects	105
Method	105
Results and Discussion	107
Experiment 2b: Assigning the colours to geometric shapes	111
Method	111
Results and Discussion	113
Experiment 3: High probability incorrectly coloured targets	115
Method	116
Results and Discussion	117
General Discussion	124
<i>Chapter 6.....</i>	<i>127</i>
<i>The unconscious binding of learned colour-form relations:.....</i>	<i>127</i>
<i>Evidence from extinction.....</i>	<i>127</i>
Synopsis	127
Introduction	128
Case Histories	131
Experiment 1: Effects of physical and learned colour	133
Materials and Methods	133
Results	137
Discussion	139
Experiment 2: Testing ipsilesional cueing	141
Method	142
Results	144
Discussion	147
General Discussion	148
<i>Chapter 7.....</i>	<i>151</i>
<i>The neural correlate of learned bindings.....</i>	<i>151</i>
Synopsis	151
Introduction	152

Method	156
Results	160
Discussion	164
<i>Chapter 8</i>	<i>166</i>
<i>General Discussion</i>	<i>166</i>
Part 1: The effects of item similarity on extinction; when and how is it beneficial?	166
Overview of the findings	166
Theoretical Implications	167
Directions for future research	169
Overview of the findings	170
Theoretical Implications	173
Alternative accounts of binding	175
Implications for current theories of object processing	175
Directions for future research	176
Overall Conclusions	177
References	179
Appendix 1	194
Appendix 2	195
Appendix 3	196

List of Illustrations

FIGURE 1: LESIONS RECONSTRUCTED FROM MRI SCANS USING VBM ANALYSIS (COMPARED TO 209 CONTROLS). SIGNIFICANT LESION ($p < 0.001$, UNCORRECTED) IS RENDERED ON A STANDARD TEMPLATE IN MRICRON WHERE DAMAGE TO GRAY MATTER IS INDICATED IN RED AND WHITE IN BLUE. MRI SCANS COULD NOT BE ACQUIRED FOR PATIENT HB.....	20
FIGURE 2: THE MEAN PROPORTION OF CONTRALESIONAL ITEMS OMITTED ON BILATERAL TRIALS. PERFORMANCE ON DISPLAYS WITH DIFFERENT ITEMS IS SUBTRACTED FROM THAT FOR DISPLAYS WITH PHYSICALLY IDENTICAL ITEMS. DATA ARE DISPLAYED SEPARATELY ALONG THE X-AXIS FOR (A) EXPERIMENT 1, (B) EXPERIMENT 2, (C) EXPERIMENT 3 AND (D) EXPERIMENT 4. EACH PATIENT IS INDICATED WITH MARKERS (AS: ○, HB: □, MP: ◇, MC: +).....	24
FIGURE 3: MEAN PROPORTION OF CONTRALESIONAL ITEMS OMITTED ON BILATERAL TRIALS. PERFORMANCE ON DISPLAYS WITH TASK-RELEVANT REPEATING ITEMS IS SUBTRACTED FROM THAT FOR DISPLAYS WITH TASK-IRRELEVANT REPEATING ITEMS.. DATA ARE DISPLAYED SEPARATELY ALONG THE X-AXIS FOR (A) EXPERIMENT 1, (B) EXPERIMENT 2, (C) EXPERIMENT 3 AND (D) EXPERIMENT 4. EACH PATIENT IS INDICATED WITH MARKERS (AS: ○, HB: □, MP: ◇, MC: +).....	25
FIGURE 4: RECONSTRUCTION OF PATIENTS' LESIONS FROM MRI SCANS. LESIONS HAVE BEEN DRAWN ONTO STANDARD SLICES FROM GADO ET AL. (GADO, HANAWAY, & FRANK, 1979). THE RIGHT HEMISPHERE IS SHOWN ON THE RIGHT. THE RIGHT FIGURE SHOWS THE 10 SLICES USED. ONLY SLICES 3 – 8 ARE DEPICTED.	40
FIGURE 5: MEAN PROPORTION OF IPSILESIONAL / RIGHT ITEM SECOND RESPONSES IS SHOWN FOR PATIENT (FILLED CIRCLES) AND CONTROL (OPEN CIRCLES) PARTICIPANTS. THIS IS PLOTTED AS A FUNCTION OF TEMPORAL ASYNCHRONY, WHICH IS EXPRESSED AS A PROPORTION OF THE STIMULUS DURATION USED TO ELICIT EXTINCTION. NEGATIVE VALUES (TO THE LEFT) INDICATE A LEAD FOR THE IPSILESIONAL STIMULUS, AND POSITIVE VALUES (TO THE RIGHT) REFLECT A CONTRALESIONAL STIMULUS ON-SETTING BEFORE AN IPSILESIONAL. LARGER VALUES REFLECT GREATER DIFFERENCES IN TEMPORAL ONSETS.	44
FIGURE 6: MEAN PROPORTION OF IPSILESIONAL ITEM SECOND RESPONSES IS INDICATED WITH AN ASTERISK (*) AND PLOTTED SEPARATELY FOR EACH EXPERIMENTAL CONDITION AS A FUNCTION OF STIMULUS ONSET ASYNCHRONY. PSYCHOMETRIC FUNCTIONS HAVE BEEN FITTED TO THESE DATA ARE DISPLAYED ALONG WITH EACH PATIENTS PSS THRESHOLD.....	45
FIGURE 7: EXAMPLES OF TWO OBJECTS IN EXPERIMENTS 1 AND 2 ARE ILLUSTRATED IN THEIR CORRECT (LEFT OF FIGURE SUB-PART) AND INCORRECT (RIGHT OF FIGURE SUB-PART) COLOURS. IN (A) THE COLOURS ARE DEPICTED ON THE SURFACE OF THE OBJECTS. IN (B) GREY-SCALE VERSIONS OF THE OBJECTS ARE SHOWN PRESENTED ON COLOURED BACKGROUNDS.....	57
FIGURE 8: RESPONSE EFFICIENCY (RT / PROP. CORR.) AND THE STANDARD ERROR OF THIS IS MEAN IS DISPLAYED FOR NAMING (A) AND RED (B) TRIAL TYPES FOR CORRECT (WHITE BARS) AND INCORRECT (GREY BARS) COLOUR CONDITIONS. MEAN EFFICIENCY SCORES ARE SEPARATED ALONG THE X-AXIS ACCORDING TO WHETHER THE COLOUR WAS DEPICTED THE ITEM'S SURFACE OR THE BACKGROUND.	59
FIGURE 9: RESPONSE EFFICIENCY IS DISPLAYED (RT / PROP. CORR.), AND THE STANDARD ERROR OF THIS MEAN, FOR NAMING (A) AND RED (B) TRIAL TYPES FOR CORRECT (WHITE BARS) AND INCORRECT (GREY BARS) COLOUR CONDITIONS. THE X-AXIS SEPARATES PERFORMANCE ACCORDING TO WHETHER THE COLOUR WAS DEPICTED ON THE ITEM'S SURFACE OR ITS BACKGROUND.	65

FIGURE 10: EXAMPLE 'RED' SURFACE AND BACKGROUND STIMULUS DISPLAYS IN EXPERIMENT 3. THE CENTRAL CROSS WAS OFFSET ON STIMULUS ONSET, BUT IS DEPICTED HERE AS A DASHED LINE TO ILLUSTRATE THE LOCATION OF FIXATION.....	71
FIGURE 11: RESPONSE EFFICIENCY IS DISPLAYED (RT / PROP. CORR.), AND THE STANDARD ERROR OF THIS MEAN, FOR NAMING (A) AND RED (B) TRIAL TYPES FOR CORRECT (WHITE BARS) AND INCORRECT (GREY BARS) COLOUR CONDITIONS. THE X-AXIS SEPARATES PERFORMANCE ACCORDING TO WHETHER THE COLOUR WAS DEPICTED ON THE ITEM'S SURFACE OR ITS BACKGROUND.	72
FIGURE 12: THE STIMULUS PAIRINGS USED IN EXPERIMENT 1.....	88
FIGURE 13: THE MEAN EFFICIENCY (RT/PROP. CORR.) FOR SEARCH FOR TARGETS IN THE CORRECT AND INCORRECT COLOURS AS A FUNCTION OF THE DIFFERENT DISPLAY SIZES (4, 8 AND 12) IN EXPERIMENT 1A. ERROR BARS = 1 SE.....	91
FIGURE 14: EXPERIMENT 1A: THE MEAN EFFICIENCY (RT/PROP. CORR.) FOR SEARCH FOR CORRECTLY COLOURED (A) AND INCORRECTLY COLOURED TARGETS (B) AS A FUNCTION OF WHETHER THE PRECEDING DISPLAY HAD A TARGET THAT WAS THE SAME COLOUR, A DIFFERENT COLOUR OR NO TARGET (ABSENT).	92
FIGURE 15: TARGET ABSENT RESPONSE EFFICIENCY IS SHOWN AS A FUNCTION OF DISPLAY SIZE AND IS SEPARATED ACCORDING TO THE APPROPRIATENESS OF THE TARGET COLOUR.(EXPERIMENT 1A)..	93
FIGURE 16: THE STIMULUS PAIRINGS USED IN EXPERIMENT 1B.	97
FIGURE 17: THE MEAN EFFICIENCY (RT/PROP. CORR.) FOR SEARCH FOR GEOMETRIC SHAPE TARGETS IN YELLOW, ORANGE AND PURPLE AS A FUNCTION OF THE DIFFERENT DISPLAY SIZES (4, 8 AND 12) IN EXPERIMENT 1B.	98
FIGURE 18: THE MEAN EFFICIENCY (RT/PROP. CORR.) ON TARGET ABSENT TRIALS FOR GEOMETRIC SHAPES (EXPERIMENT 1B). NON-TARGET STIMULI SETS WERE DIVIDED ACCORDING TO THE TARGET PAIRINGS (YELLOW, ORANGE AND PURPLE SQUARES). PERFORMANCE IS DISPLAYED AS A FUNCTION OF DISPLAY SIZE (4, 8 AND 12).	99
FIGURE 19: EXAMPLE STIMULI FROM EXPERIMENT 1C. THE TARGETS ARE SHOWN ON THE LEFT (CORN) AND THE NON-TARGETS PRESENTED WITH EACH TARGET ARE DEPICTED IN THE SAME ROW.....	102
FIGURE 20: TARGET PRESENT TRIALS IN EXPERIMENT 1C, WITH OBJECTS DEPICTED ON BACKGROUNDS THAT WERE OR WERE NOT THE CORRECT COLOURS FOR THE REAL STIMULI	103
FIGURE 21: MEAN EFFICIENCY OF PERFORMANCE IN EXPERIMENT 1C (BACKGROUND COLOURS)	104
FIGURE 22: EXAMPLE STIMULI FROM EXPERIMENT 2A. THE TARGET IS SHOWN ON THE LEFT OF EACH FIGURE AND THE NON-TARGETS APPEARING ALONG WITH IT ARE DEPICTED ALONG EACH ROW. ROWS 1 AND 3 CORRECT TARGET, ROWS 2 AND 4 INCORRECT TARGET. ROWS 1 AND 2 CORRECT NON-TARGETS; ROWS 3 AND 4 INCORRECT NON-TARGETS. THE DISPLAYS WERE SELECTED AT RANDOM.....	106
FIGURE 23: EXPERIMENT 3. THE MEAN EFFICIENCY FOR SEARCH FOR CORRECTLY AND INCORRECTLY COLOURED TARGETS ACCORDING TO WHETHER THE ACCOMPANYING NON-TARGETS WERE CORRECTLY (A) OR.....	107
FIGURE 24: SEARCH EFFICIENCY AVERAGED ACROSS THE THREE DISPLAY SIZES. NON-TARGET COLOUR-SHAPE PAIRING IS DISPLAYED ON THE X-AXIS, AND PERFORMANCE IS SEPARATED ACCORDING TO THE APPROPRIATENESS OF THE TARGET COLOUR (EXPERIMENT 2A).	108
FIGURE 25: MEAN SEARCH EFFICIENCY TARGET ABSENT TRIALS AS A FUNCTION OF THE COLOURS OF THE NON-TARGETS (EXPERIMENT 2B)	105
FIGURE 26: THE STIMULUS PAIRINGS USED IN EXPERIMENT 2B. THE TARGET WAS EITHER 'CORRECT' (RED) OR 'INCORRECT' (PURPLE), AND THE NON-TARGETS WERE ARBITRARILY CODED AS 'CORRECT' (TOP TWO LINES; RED AND GREEN OVALS) OR 'INCORRECT' (BOTTOM TWO LINES; RED AND PURPLE OVALS).	112

FIGURE 27: EFFICIENCY SCORES FOR SEARCH FOR CORRECT (RED) OR INCORRECT (PURPLE) COLOURED TARGETS AS A FUNCTION OF THE COLOUR OF THE NON-TARGETS ((A) CORRECT – RED AND GREEN OVALS; (B) INCORRECT – RED AND PURPLE OVALS) (EXPERIMENT 2B).....	113
FIGURE 28: MEAN EFFICIENCY SCORES ON TARGET ABSENT TRIALS AS A FUNCTION OF THE COLOURS OF THE NON-TARGETS (EXPERIMENT 2B)	114
FIGURE 29: EXPERIMENT 3: THE MEAN EFFICIENCY (RT/PROP. CORRECT) FOR SEARCH FOR CORRECTLY COLOURED TARGETS (A) AND FOR INCORRECTLY COLOURED TARGETS (B), WHEN THERE WAS A PRESENTATION BIAS FAVOURING THE INCORRECTLY COLOURED TARGETS. PERFORMANCE IS SHOWN AS A FUNCTION OF THE PRECEDING TRIAL: TARGET SAME COLOUR, TARGET DIFFERENT COLOUR, TARGET ABSENT.....	118
FIGURE 30: TARGET ABSENT RESPONSE EFFICIENCY IS SHOWN AS A FUNCTION OF DISPLAY SIZE, AND IS SEPARATED ACCORDING TO THE APPROPRIATENESS OF THE TARGET COLOUR (CORRECT OR INCORRECT; EXPERIMENT 3)	119
FIGURE 31: THE NUMBER OF FIXATIONS TO THE DIFFERENT COLOURED ITEMS, SUMMED ACROSS ABSENT AND PRESENT TRIALS, SCALED FOR THE DIFFERENT PROPORTIONS ON TRIALS FOR CORRECT AND INCORRECTLY COLOURED TARGETS. THE LEMON COULD BE YELLOW (CORRECT) OR PURPLE (INCORRECT). THE CARROT COULD BE ORANGE (CORRECT) OR PURPLE (INCORRECT). THE AUBERGINE COULD BE PURPLE (CORRECT) OR ORANGE (INCORRECT). PERFORMANCE HERE IS AVERAGED ACROSS THE DISPLAY SIZES (EXPERIMENT 3).	120
FIGURE 32: THE RATIO OF FIXATIONS ON PURPLE RELATIVE TO YELLOW COLOR NON-TARGETS (CARROTS AND AUBERGINES), NORMALIZED BY THE FIXATIONS TO BOTH NON-TARGETS WHEN THEY WERE ORANGE (A MEASURE OF THE SHAPE SIMILARITY OF EACH NON-TARGET TO THE TARGET). THE RATIO OF FIRST FIXATIONS TO PURPLE RATHER THAN YELLOW NON-TARGETS WAS APPROXIMATELY 2:1	121
FIGURE 33: MEAN FIXATION DURATIONS (DWEIL TIME) TO STIMULI CARRYING A TARGET COLOUR (YELLOW OR PURPLE).	122
FIGURE 34: MEAN NUMBER OF RE-FIXATIONS WITHIN A TRIAL TO CORRECTLY AND INCORRECTLY COLOURED TARGETS AS A FUNCTION OF THE DISPLAY SIZE	123
FIGURE 35: LESION CREATED USING VBM ANALYSIS OF T1 SCANS USING A ONE-SAMPLED T-TEST IN SPM. THIS INCLUDED 3 COVARIATES: AGE, GENDER, ACQUISITION LOCATION (BUIC / OASIS) HEALTHY (209, AGE RANGE 40-87) VS. PATIENT. SITES SHOWING A SIGNIFICANT CHANGE IN IMAGE INTENSITY RELATIVE TO THE CONTROLS (FWE 0.001, >100 VOXELS) ARE RENDERED ON A STANDARD TEMPLATE IN MRICRON WHERE RED INDICATES GREY MATTER AND BLUE WHITE MATTER DAMAGE. SCANS WERE NOT AVAILABLE FOR DB.....	132
FIGURE 36: EXAMPLE STIMULUS PAIRINGS ON TWO-ITEM TRIALS. HERE, THE CONTRALESIONAL (LEFT) ITEM IS A CORRECTLY COLOURED GREEN LETTUCE DEPICTED IN EACH OF THE FOLLOWING CONDITIONS: (A) <i>SAME SHAPE, SAME COLOUR</i> , (B) <i>SAME SHAPE, DIFFERENT COLOUR</i> , (C) <i>DIFFERENT SHAPE, SAME COLOUR</i> , (D) <i>DIFFERENT SHAPE, DIFFERENT COLOUR</i>	134
FIGURE 37: EXAMPLE STIMULUS PAIRINGS ON TWO-ITEM TRIALS. HERE, THE CONTRALESIONAL (LEFT) ITEM IS A INCORRECTLY COLOURED PURPLE LETTUCE DEPICTED IN EACH OF THE FOLLOWING CONDITIONS: (A) <i>SAME SHAPE, SAME COLOUR</i> , (B) <i>SAME SHAPE, DIFFERENT COLOUR</i> , (C) <i>DIFFERENT SHAPE, SAME COLOUR</i> , (D) <i>DIFFERENT SHAPE, DIFFERENT COLOUR</i>	135
FIGURE 38: MEAN PROPORTION CORRECT REPORTS ON ONE- AND TWO-ITEM TRIALS ACCORDING TO WHETHER THE CONTRALESIONAL STIMULUS WAS CORRECTLY COLOURED OR NOT.....	137
FIGURE 39: MEAN PROPORTION CORRECT IN EACH OF THE TWO-ITEM TRIAL CONDITIONS. THESE ARE: SAME SHAPE-SAME COLOUR (SS-SC), SAME SHAPE-DIFFERENT COLOUR (SS-DC), DIFFERENT SHAPE-SAME COLOUR (DS-SC), AND DIFFERENT SHAPE-DIFFERENT COLOUR (DS-DC). THE COLOUR-SHAPE CONSISTENCY OF THE CONTRALESIONAL ITEM IS INDICATED BY THE BAR COLOUR. ERROR BARS INDICATE THE STANDARD ERROR OF THE MEAN.	138
FIGURE 40: EXAMPLE STIMULUS PAIRINGS ON TWO-ITEMS TRIALS WHERE THE CONTRALESIONAL (HERE LEFT) STIMULUS IS COLOUR CONGRUENT (GREEN LETTUCE). (A) <i>SAME COLOUR, BOTH</i>	

<i>CORRECT, (B) SAME COLOUR, IPSILESIONAL-INCORRECT, (C), DIFFERENT COLOUR, BOTH CORRECT, (D) DIFFERENT COLOUR, IPSILESIONAL-INCORRECT.</i>	143
FIGURE 41: EXAMPLE STIMULUS PAIRINGS ON TWO-ITEMS TRIALS WHERE THE CONTRALESIONAL (HERE LEFT) STIMULUS IS COLOUR INCONGRUENT (RED LETTUCE). (A) <i>SAME COLOUR, BOTH CORRECT, (B) SAME COLOUR, IPSILESIONAL-INCORRECT, (C), DIFFERENT COLOUR, BOTH CORRECT, (D) DIFFERENT COLOUR, IPSILESIONAL-INCORRECT.</i>	143
FIGURE 42: MEAN PROPORTION CORRECT ON ONE- AND TWO-ITEM TRIALS ACCORDING TO THE COLOUR-SHAPE CONSISTENCY. NOTE THAT WHEN CONSIDERING TWO-ITEM TRIALS THE COLOUR CONDITION REFLECTS THE COLOUR-SHAPE CONSISTENCY OF THE CONTRALESIONAL STIMULUS...	144
FIGURE 43: MEAN PROPORTION OF CONTRALESIONAL ITEMS CORRECTLY IDENTIFIED WHEN THE IPSILESIONAL ITEM WAS CORRECTLY (A) OR INCORRECTLY (B) COLOURED. THIS IS DISPLAYED WHEN THE COLOUR IS THE SAME FOR BOTH ITEMS, AND THIS IS THE CORRECT (WHITE BARS) OR INCORRECT (GREY BARS) HUE FOR THE CONTRALESIONAL STIMULUS.	145
FIGURE 44: EXAMPLE OF ONE STRAWBERRY STIMULUS ILLUSTRATED IN ITS CORRECT (LEFT OF FIGURE SUB-PART) AND INCORRECT (RIGHT OF FIGURE SUB-PART) COLOURS. THE LOWER PART OF THE FIGURE THE ITEMS ARE SCRAMBLED.	157
FIGURE 45: MARKED IN RED ARE THOSE REGIONS THAT ARE SIGNIFICANTLY MORE ACTIVATED BY INTACT RELATIVE TO SCRAMBLED ITEMS, AND IN BLUE THOSE REGIONS SHOWING THE REVERSE OF THIS CONTRAST.	160
FIGURE 46: MARKED IN RED ARE THOSE REGIONS THAT ARE SIGNIFICANTLY MORE ACTIVATED BY INTACT RELATIVE TO SCRAMBLED ITEMS, AND IN BLUE THOSE REGIONS SHOWING THE REVERSE OF THIS CONTRAST.	161
FIGURE 47: INTACT ITEMS INCORRECTLY > CORRECTLY COLOURED: (A) OVERLAID ON A SAGITAL VIEW OF THE MNI CANONICAL BRAIN. (B) RENDERED ON AN INFLATED BRAIN MESH, SHOWING THE INFERIOR VIEW. (C) BAR GRAPH SHOWING THE EFFECT SIZE (BOLD SIGNAL CHANGE RELATIVE TO THE GLOBAL BRAIN MEAN) AT THE SITE OF PEAK ACTIVATION WITHIN THIS CLUSTER FOR ALL FOUR EXPERIMENTAL CONDITION. ERROR-BARS INDICATE 90% CONFIDENCE INTERVALS.	163

List of Tables

TABLE 1: STIMULUS DURATION (MS) FOR EACH PARTICIPANT IN ALL EXPERIMENTS.....	22
TABLE 2: PERCENTAGE OF CONTRALESIONAL STIMULI CORRECTLY IDENTIFIED WHEN PRESENTED IN ISOLATION (UNILATERAL) AND SIMULTANEOUSLY WITH AN IPSILESIONAL ITEM (BILATERAL) AT THE STIMULUS DURATION SPECIFIED. THE PSS (POINT OF SUBJECT SIMULTANEITY) AND JND (JUST NOTICEABLE DIFFERENCE) FOR EACH PATIENT IN GROUPING AND NON-GROUPING EXPERIMENTAL CONDITIONS ARE DISPLAYED IN THE LAST FOUR COLUMNS.	41
TABLE 3: SPEECH PRODUCTION LATENCIES AND THE PROPORTION OF CORRECT RESPONSES FOR 'NAMING' TRIALS. THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	60
TABLE 4: SPEECH PRODUCTION LATENCIES AND PROPORTION CORRECT RESPONSES FOR 'RED' TRIALS. THE RESULTS ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	61
TABLE 5: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT RESPONSES FOR 'NAMING' TRIALS. THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	66
TABLE 6: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT RESPONSES FOR 'RED' TRIALS. THE RESULTS ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	67
TABLE 7: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT RESPONSES FOR 'NAMING' TRIALS. THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	73
TABLE 8: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT FOR 'RED' TRIALS. THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	74
TABLE 9: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT FOR NAMING COLOURS (EXCLUDING 'RED'). THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	75
TABLE 10: SPEECH PRODUCTION LATENCY AND PROPORTION CORRECT FOR COLOUR NAMING RED TRIALS. THE DATA ARE DISPLAYED FOR CORRECTLY AND INCORRECTLY COLOURED STIMULI ACCORDING TO WHETHER THE HUE WAS DEPICTED ON THE ITEM'S SURFACE OR BACKGROUND.	76
TABLE 11: NUMBER OF SESSIONS COMPLETED, AND THE STIMULUS DURATION USED FOR EACH PATIENT.	136
TABLE 12: PROPORTION OF INCORRECT TRIALS WHERE PATIENTS MADE AN ERRONEOUS RESPONSE (RATHER THAN AN OMISSION).	139
TABLE 13: NUMBER OF SESSIONS COMPLETED, AND THE STIMULUS DURATION USED FOR EACH PATIENT.	144
TABLE 14: PROPORTION OF INCORRECT TRIALS WHERE PATIENTS MADE AN ERRONEOUS RESPONSE (RATHER THAN AN OMISSION).	146
TABLE 15: CLUSTER SIGNIFICANT AT WHOLE BRAIN CORRECTED FOR MULTIPLE COMPARISONS AT 0.05 LEVEL.....	162
TABLE 16: PROPORTION OF OMISSIONS WHEN ITEMS ARE IDENTICAL (IN BOTH SHAPE AND COLOUR) COMPARED WITH WHEN THEY WERE DIFFERENT (IN BOTH SHAPE AND COLOUR).	194
TABLE 17: PROPORTION OF OMISSIONS WHEN ONLY THE TASK RELEVANT FEATURE WAS REPEATED VS. NOT REPEATED.	194

Preface

Chapter 2: Some of the data presented has been published in the following book chapter: Riddoch, M. J., Rappaport S. J, Humphreys, G. W (2009), Extinction: a window into attentional competition. In Srinivasan N. (Ed), Attention, pp 149-161. Progress In Brain Research, Elsevier, Oxford, UK.

Chapter 3: This chapter has been published as a brief communication in Neuropsychologia. Rappaport, S. J., Riddoch, M. J. & Humphreys, G. W. (2011), 49, 151-155. The introduction has been amended to avoid repetition from Chapter 2.

Chapter 4: Melanie West collected the data presented in Experiment 4. These experiments were presented at the European Conference of Visual Perception 2011. This chapter is currently under review at Journal of Experimental Psychology: Learning, Memory and Cognition.

Chapter 5: Glyn Humphreys and Jane Riddoch collected the data presented in Experiment 1c and 2b. This data was presented at the Vision Sciences Society, 2011. This chapter has been accepted for publication by The Journal of Experimental Psychology: Human Perception and Performance.

Chapter 6: MatLab routines for stimulus colour inversion were developed in conjunction with Dirk Ostwald.

Chapter 7: Routines to generate scrambled versions of correctly and incorrectly coloured stimuli were developed in conjunction with Harriet Allen. This chapter is currently under review at Visual Cognition.

CHAPTER 1: GENERAL INTRODUCTION

The Binding Problem

The ease with which we perceive the world as unitary and coherent belies the difficulty this task presents to our visual system. Consider for example a simplified scene of a red triangle and a blue square moving around the display. To perceive this ‘simple’ display requires parsing of the basic elements and coding of how distributed information about colour, shape, trajectory etc. are combined, to enable the perceiver to know that the red triangle is moving eastwards. There is considerable evidence from neurophysiology, brain imaging and neuropsychology that the early stages of visual processing segregate the image into independent features. For example, seminal physiological evidence by Hubel and Livingstone (1987) reported that the visual system was divided into distinct parvo- and magnocellular channels, with the different features of stimuli (their color, shape, motion) being processed in distinct brain regions. Single cell recordings have demonstrated that, within the visual cortex, there are specialised areas where cells selectively respond to a given feature so that (e.g.) cells in V4 show colour rather than motion selectivity whilst cells in area MT have the opposite stimulus selectivity (Zeki 1973; 1974; 1977). Consistent with this, fMRI studies have shown functional specialisation within the brain where different features are processed in distinct cortical regions (see Kanwisher, 2010), while damage to the distinct regions can generate selective problems in processing particular visual features (e.g., see papers in Humphreys, 1999). Despite this segregation, our perception of the world is coherent and unified. This raises the ‘binding problem’; how is distributed information put back together? In this thesis I

consider two ways in which the brain may overcome the binding problem: Part 1 pre-attentive grouping and Part 2 learned binding between associated features.

Binding Solutions

i) Complex Cells

Nobel prize winning electrophysiology research by Hubel and Wiesel (1959, 1962, 1968) inspired a feed-forward solution to the binding problem. From single cell recordings in the cat they proposed that there is a hierarchy of neurons advancing from specialised features maps in the initial stages of cortical vision, to increasingly complex representations integrating information computed at the initial stages. Evidence for combination coding cells at advance stages in the visual processing stream support this model (see Van Essen and Gallant, 1994). Hubel and Weisel (1962) reported apparent invariance in higher-level neurons that responded to a stimulus across different transformations e.g. different positions. Similarly Gross et al., (1972) reported single cell recordings in the macaque infer-temporal cortex preferentially responding to a monkey's hand. Barlow (1972) adopted this hierarchy suggesting 'cardinal', also known as 'grandmother', cells. This remedy however is flawed by a 'computational explosion' problem. More specifically, there are essentially an unlimited number of potential conjunctions of visual features, and the idea that each requires a specialised individual coding processor was deemed unfeasible.

ii) Temporal Synchrony

In response to the inflexibility and computational limitations of the specialised higher-order binding units, the temporal account of binding developed. Stemming from Von der Malsburg's (1981) suggestion that that brain could exploit temporal synchrony to bind features, Gray et al. (1989; 1992) provided physiological evidence of precise synchronization

of neural discharges to grouped features in the striate cortex of the cat. Recordings were made from spatially separate columns, which exhibited different orientation preferences. Gray and colleagues compared activation when two light bars moved together relative to when they moved independently. Across the recording sites, the activation of neurons responding to common motion were synchronized to within a few milliseconds, ‘tagging’ each neuron in a cell assembly. Recent EEG recordings have similarly shown precise temporal synchrony of oscillations to grouped items (Tallon-Baudry et al 2001). Temporal binding provides a flexible solution that does not rely on combination coding, and is consistent with the conception of the brain as a distributed network. It is the transience of synchronized coding, however, that is also its main shortcoming. Temporal correlation is a fleeting marker to bind features, but how then do we know about the binding once the stimuli are removed? Our subjective perception is that we have an enduring representation of stimuli we have interacted with, but the temporal binding theory does not suggest any residual trace allowing for permanence. On the other hand, there is evidence that visual features are bound in visual short-term memory (Luck & Vogel, 1997). Furthermore, this model cannot easily account for how the features of multiple different objects can be bound together in a complex scene, when multiple potential binding relationships are possible (Shadlen & Movshon, 1999). Consider again the simple scene example of a red triangle and blue square. Synchrony may signal feature clusters but how would we know which belongs to each object and how are they localised in space? Finally this account is not clearly supported by neurological evidence of binding impairments following parietal damage. It is difficult to conceive how these data can be reconciled within a temporal correlation hypothesis, since if binding is computed by synchrony in the visual cortex, why then would it be disrupted by parietal damage? I will discuss a more parsimonious account of visual binding deficits in the next section.

As with models proposing specialised conjunction-coding cells, physiological data clearly demonstrate that temporal coherence is important and cannot be dismissed, however, in isolation, temporal coding does not sufficiently answer the binding problem.

iii) Attention – Feature Integration Theory

Treisman and Gelade's influential (1980) Feature Integration Theory (FIT) solves the binding problem by proposing that binding is achieved through the engagement of spatial attention upon a stimulus. This account was largely developed from visual search studies, where participants have to detect an item within an array of non-targets. It has been repeatedly reported that there is a contrast between efficient 'pop-out' of a target defined by a feature difference relative to distractors, along with inefficient search for a target defined by a unique conjunction of the features (even when the individual features themselves 'pop out') (see Treisman 1988, 1996, 1999 for overviews). For example, detection of a red item amid an infinite number of green distractors is seemingly effortless. In contrast, detection of a red-vertical bar in an array of green-vertical and red-horizontal bars is inefficient and becomes increasingly difficult as more non-targets are added to the array. Treisman and Gelade argued for a sequential two-stage account of binding. Firstly feature-maps code the presence of a feature along a particular dimension (colour, orientation, motion) in an initial parallel processing stage. These maps are retinotopically organised in early striate and extra-striate areas. Using the above visual search example, the red item 'pops-out' against the green items because it uniquely activates its one colour feature-map. More complicated conjunctions of elements (as in the red vertical example) however require integration and binding across 'feature-maps' to generate 'object-files', and this is mediated by attention. Essentially by spatially attending to only one stimulus at a time, there is activation only of the attend features at the object file level and reduced chance of illusory bindings between the features of the other stimuli present. That is, the binding problem is solved.

Complimentary evidence comes by considering the effects on binding when attention is restricted. Treisman and Schmidt (1982) created this scenario by presenting participants with multiple coloured shapes flanked by two black digits. Participants were primarily required to attend to and report the numbers, and afterwards the coloured shapes. Treisman and Schmidt found that participants mis-combined features of the objects, so giving rise to ‘illusory conjunctions’. For example, participants might erroneously recombine the shape and colour features by reporting a green circle when a green square and red circle were presented. As FIT would predict under conditions of suboptimal attention, binding was compromised. Within the FIT framework one would expect that a reduction in spatial attention would give rise to feature binding problems. Indeed there is converging evidence for this. Following unilateral parietal damage patients pathologically fail to attend to one side of space. The patients are also unusually prone to making illusory conjunctions, and in the context of a visual search task, they can detect targets defined by a feature but are impaired when features must be combined (Friedman-Hill, Robertson, Treisman, 1995). Since its conception FIT has been supported by an extensive literature and has dominated accounts of binding in perception, emphasising the critical role of attention.

Different forms of binding

Although the FIT theory has been developed over a time period, its central claim that all binding requires spatial attention has endured. The idea of a unitary binding mechanism however is not easily reconciled with findings of i) pre-attentive binding and ii) differences between within and across domain binding.

i) Pre-attentive Binding

There is evidence for binding without attention. Consider again the assay of processing without attention: patients suffering from visual extinction. Typically extinction patients omit a stimulus on the unattended contralesional side of space, pathologically favouring the ipsilesional item. Grouping between items however can modulate the severity of the extinction deficit. For example, Ward and colleagues (Ward, et al., 1994) demonstrated extinction when a contralesional square bracket was accompanied by an ipsilesional dot, but not when the ipsilesional stimulus was another, symmetrical bracket that grouped by symmetry, collinearity and closure with the contralesional bracket. Similar effects of low-level grouping on extinction have subsequently been reported using an extensive range of factors including common colour, surface polarity, brightness and enclosure (Gilchrist et al., 1994, Mattingley et al., 1997, Humphreys 1998 for an overview).

Grouping effects on extinction are not confined to low-level properties of stimuli. There is evidence that stimulus familiarity can also influence grouping effects on extinction. Ward et al. (1994) used elements that did not share any low level features but could be orientated into a familiar configuration. They reported reduced extinction when elements grouped into an arrow relative to when they did not group (- > vs. | >). Kumada and Humphreys (2001) reported complimentary results using letter stimuli. Again low-level grouping was equated and yet extinction was reduced when the contra- and ipsilesional items formed a word (g o) relative to a non-word (o g). These results indicate that prior engaging serial attention some form of binding of visual elements has taken place.

In Part 1 of this thesis I report neuropsychological studies examining binding processes in extinction patients, and I will review how binding can be exploited to overcome the extinction deficit.

ii) Within vs. Across Feature Domain

In the discussion thus far there has been no distinction made between different forms of binding. For example, would we expect any difference between binding different elements into a shape (within domain form binding) vs. binding shape and colour (across domain)? Both the FIT and temporal synchrony account would not since binding is thought to operate irrespective of the nature of the feature dimension. Humphreys et al. (2000, 2009) studied a patient GK who had suffered bilateral parietal damage. They reported dissociation between binding across vs. within dimensions. GKs form binding was intact, however he showed impairment when binding colour and form.

An alternative multistage theory has developed to account for such findings (Humphreys et al. 2009). Within this framework, in the first stage of binding form elements are grouped into objects based on bottom-up grouping and top-down re-entrant processing of stored object representations. In a second-stage spatial attention is engaged and bindings across feature domains are made and initial conjunctions established. This would account for deficits such as those found in patient GK in terms of him having the first form-based stage of binding intact, but the second stage, of binding across form and surface details, impaired.

Effects of stored knowledge on binding

Nearly all studies examining binding in visual perception have focused on the integration of features that have no prior association. However the principles that govern the binding of arbitrary features may not apply to more complex real-life stimuli. In our environment many

objects do not have arbitrary feature relations but have consistent and set associations. How are these features bound? Is the binding of learned features be-set by the limitations that affect the binding of arbitrary features? Here I address the ‘binding problem’ by considering a scenario more characteristic of our environment, focusing on the binding of ‘diagnostic’ colour and form. A colour is said to be diagnostic if it is a consistent property of the object; for example, yellow is ‘diagnostic’ of a banana but not a bicycle. It seems plausible that the brain may exploit such regularities to develop some form of ‘hardwired’ coding of learned feature relations.

There is evidence that fits with the idea that the binding of learned associations operates rapidly. Using a dual-task procedure, Li et al. (2002) found that a central attentionally demanding letter discrimination did not compromise the ability of participants to detect a briefly presented peripheral animal or vehicle. Analogous results have been found using face stimuli requiring either gender discrimination (Reddy et al., 2004) or face recognition (Reddy et al., 2006). This suggests that coding the relations between the features making up these stimuli, to enable identification to proceed, can take place without deploying attention. Van Rullen (2009) proposed that this was achieved by ‘hardwired binding’, which integrates features of familiar natural scenes and objects automatically and without serial attention. He argued that this mechanism co-exists with an ‘on-demand’ system dealing with arbitrary and unfamiliar conjunctions by engaging visual attention.

Naor-Raz et al (2003) found that participants reported the colour of an item more quickly when it was congruent with its shape than when it was incongruent. For example, the colour of a banana could be reported more quickly when it was yellow than when it was purple. Further corroborating evidence comes from human electrophysiological recordings, which have revealed ERP components indexing relatively early perceptual processing (N1, N2 and

P2) differentiate between correctly coloured stimuli and incorrect and gray-scale versions of the same items (Lu et al., 2010). Similarly single cell recordings in the macaque superior temporal sulcus and inferior temporal cortex show sensitivity to colour-shape congruency. These differences between correctly and incorrectly coloured stimuli are seen in the fastest responses (~91ms), again implicating early processes in binding learned conjunctions. Recent fMRI evidence also supports a distinction between the coding of arbitrary and learned feature bindings; whilst parietal areas have been associated with binding arbitrary feature learned relations (Donner et al., 2002; Wardak, Olivier, Duhamel, 2004) learned feature relations may be supported by temporal regions (Walsh et al., 1998; Frank et al., 2011; Zeki and Marini, 1998) The brain mechanisms of binding learned features are considered in more detail in Chapter 7. Cumulatively the findings highlight that, when colour is a consistent property of an object, it is stored in the object's perceptual representation, facilitating object recognition. Whether, and how, learned colour and form relationships interact with attention has not been comprehensively examined.

There is some limited evidence from the visual attention literature that would also suggest colour may form an intrinsic part of an object's representation and is coded pre-attentively. Preliminary evidence using illusory conjunctions was reported by Treisman in an early review article (1986) and again in a *Bartlett Lecture* to the *Experimental Psychological Society* (1988). As I have discussed above, under conditions of limited attention object features can be incorrectly bound, so that a blue circle is erroneously reported when a red circle and a blue square are briefly presented. Treisman documented that such conjunction errors were constrained when items were labelled and presented in their congruent colour (e.g. an orange triangle labelled as a carrot). These results suggest that associated colour and shape features may be bound without the deployment of attention and are therefore not available for erroneous recombination. Further evidence for this proposal comes from a recent study by

Olivers (2011). Participants viewed a search array of eight well-known traffic signs and were required to detect the one specified. All the stimuli were presented in gray-scale (including the target) except one distracter that was presented in full colour. Critically, the colour of this distracter could be either be related (e.g. red, when the target is a stop-sign) or unrelated (e.g. yellow, when the target is a stop-sign) to the target stimulus. Participants' target detection was faster when the colour of the distracter was unrelated to the target than when it was related. Similar to the Stroop Effect, this finding indicates that when activating a target template we retrieve both relevant attributes and irrelevant but strongly associated information. Here this manifests as automatic activation of colour information strongly associated with the target but entirely irrelevant to this task, which captured attention and guided visual search. This again indicates that long-term associations between colour and form exert an influence at an early stage of processing.

Colour effects in object recognition

The binding between 'diagnostic' colour and form is relevant to the object processing literature, where the role of colour is crucial in the debate between 'edge-' and 'surface-plus-edge-' based accounts. Early, and still influential, theories of object processing emphasise the importance of form in identification, arguing that recognition is achieved by decomposition of objects into simple volumetric components (Biederman 1987, Marr 1982). Surface information is relegated to a late stage of processing or to resolve ambiguity in conditions of degradation (Nicholson & Humphrey, 2001; Wurm, Legge, Isenberg, & Luebker, 1993). Supporters of this model cite studies showing that achromatic line drawings can be recognised as quickly as full-colour depictions (Biederman and Ju, 1988). These studies have been criticised however based on the stimuli-set; for example, of the twenty-nine stimuli used by

Biederman and Ju (1988) only five had a diagnostic colour (e.g. apple) and most were metallic (e.g. classic telephone) or achromatic (e.g. fork).

Clearly form is important in object recognition but whether the primary mental representation of an object is achromatic has been contentious. ‘Surface-plus-edge’ accounts argue that colour is an intrinsic part of an objects representation, interacting with shape from the earliest stage of processing. In one such model proposed by Davidoff and de Bleser (1993) and Davidoff (2001) the first stage (temporal register) of processing shape boundaries includes surface (and therefore colour) information. Tanaka, Weiskopf and Williams’ (2001) ‘Shape + Surface’ model includes perceptual inputs from shape, texture and colour, thus representing objects by all of these features. Considering only the contribution of ‘diagnostic’ colour in object recognition (Tanaka, Weiskopf et al. 2001) there is increasingly convergent findings; objects depicted in their standard colour are recognised faster and more accurately than gray-scale or incorrectly coloured versions (Price & Humphreys, 1989; Tanaka & Presnell, 1999; Wurm et al., 1993). Indeed the aforementioned studies emphasising the automaticity and speed of congruent-colour processing suggests that diagnostic colours could form part of an object’s perceptual representation, being bound at an early stage of processing (Davidoff, 2001; Tanaka, Weiskopf, & Williams, 2001). This would provide support for the ‘surface-plus-edge’ rather than ‘edge-’ based hypothesis.

It is however important to note that neuropsychological studies seem to suggest that knowledge of object shape and colour may be dissociable. One such case reported by Riddoch and Humphreys (1987) detailed patient J.B. who was able to make difficult object-decisions but wasn’t able to decide whether objects were correctly coloured or not. Another patient, I.O.C showed preserved knowledge of object form and colour, and yet his object-colour knowledge was impaired (Miceli et al., 2001). Such examples suggest a degree of

independence between colour-knowledge, object-shape-knowledge and object-colour knowledge. This may be difficult to reconcile with arguments that colour and shape form part of an integrated representation of an object's visual characteristics. However, it is of course possible that tests sensitive to implicit processing may yield different results. Indeed Nijboer et al. (2006) reported that although patient M.A.H was unable to identify or categorise colours, on tests of implicit processing he showed effects of colour congruency indicating automatic processing of colour. Applying similar implicit measures to cases of selective object-colour knowledge would be valuable.

In Part 2 I use four complimentary methodologies to examine the binding of learned colour-form relations. In Chapter 4, I employ a modified Stroop paradigm to ask whether colour and shape are automatically unitised when they have a learned relationship. Chapter 5 presents a series of visual search experiments, a paradigm at the crux of binding accounts such as FIT, to examine whether selection is guided by learned feature conjunctions. In Chapter 6 a visual extinction paradigm was employed as an assay of pre-attentive processing, and I tested whether learned associations are processed in the contralesional hemi-space. Finally, in Chapter 7 I used fMRI to examine the neural correlates of learned bindings. The findings I will present provide clear evidence for learned feature bindings being coded pre-attentively, without involvement of the posterior parietal cortex associated with spatial attention.

**Part 1: The effects of item similarity on
extinction; when and how is it beneficial?**

CHAPTER 2: FROM HELPING TO HURTING: SHIFTING THE EFFECTS OF SIMILARITY ON VISUAL SPATIAL BIASES IN EXTINCTION

Synopsis

The effect of stimulus similarity on extinction remains controversial, with seemingly contrary reports of both beneficial effects of similarity-based grouping (Ward, Goodrich et al. 1994; Gilchrist, Humphreys et al. 1996) and detrimental affects of task-relevant repetitions (Baylis, Driver et al. 1993; Baylis, Gore et al. 2001; Rafal, Danziger et al. 2002). I assessed the effects of stimulus eccentricity and the presence of a central fixation cross on the apparently discrepant results. In the same patients, similarity was found to increase extinction when the stimuli were presented at relatively large eccentric locations (12°) and when a central fixation cross remained throughout the trial. In contrast, similarity reduced extinction in the same patients when stimuli were presented closer to fixation (3.4°) and the fixation cross was offset when the critical stimuli appeared. These findings suggest that (i) stimulus similarity mitigates visual-spatial biases when arrays promote perceptual grouping, but (ii) can exacerbate spatial deficits in selection when the array parameters encourage stimuli to be selected consecutively and processed as distinct distal elements.

Introduction

Visual extinction is a neurological disorder characterised behaviourally by successful detection and identification of a stimulus on the contralesional side when it is presented in isolation, but a failure to do so once it is accompanied by an ipsilesional item (Karnath, 1988). Current theories of visual attention consider extinction to be a pathological bias of the normal competition for selection in favour of the ipsilesional item (Duncan & Humphreys, 1992; Duncan, Humphreys, & Ward, 1997; Duncan & Humphreys, 1989).

A key principle in the ‘competition’ framework of visual attention is ‘weight-linkage’. It is argued that, when visual elements form a single group, then their ‘attentional weight’ is shared so that the elements no longer compete for selection (Bundesen, 1990; Duncan & Humphreys, 1989). In patients with spatial biases there may be increased attentional weight to the ipsilesional side at the expense of contralesional stimuli (Duncan et al., 1997). This bias may be mitigated, though, if the attentional weight of the ipsilesional stimulus can be shared with the contralesional item, if the elements group. Under these conditions, extinction should reduce. Initial evidence presented by Ward, Goodrich and Driver (1994) confirmed this possibility. They demonstrated improved detection of a contralesional bracket when paired with a collinear, ipsilesional bracket rather than a dot. The authors proposed that the two brackets grouped by the Gestalt principles of symmetry, collinearity and closure and were selected together by a process of weight-linkage. An extensive range of low-level grouping features have since been reported to benefit successful perceptual report, enumeration, detection and localisation of the contralesional stimulus (Gilchrist, Humphreys, & Riddoch, 1996; Humphreys, 1998; Pavlovskaya, Sagi, & Soroker, 2000; Pavlovskaya, Sagi, Soroker, & Ring, 1997; Ward et al., 1994).

In apparent conflict with these findings, detrimental effects of similarity have also been documented. Baylis, Driver and Rafal (1993) were the first to report that repetition of a task-relevant feature could exacerbate extinction. On two-item trials, patients were presented with coloured letter stimuli that could be identical or differ in shape and/or colour. Patients were required to report either the colour or the shape and side of presentation of the stimulus. Extinction was increased when the contralesional and ipsilesional items matched along the required response dimension. For example, when required to report colour, a green contralesional item was omitted more frequently when paired with a green rather than a red ipsilesional stimulus. The authors noted that this effect is similar to the ‘repetition blindness’ reported in normal participants whereby accuracy is negatively affected by item similarity. For example, Kanwisher (1991) showed that, under conditions of brief sequential visual presentations, normal participants failed to detect a second incidence of a target previously attended to (e.g., missing the second ‘a’ in the word ‘manager’ and instead incorrectly reported ‘manger’). This pattern has been suggested to reflect a failure in rapidly generating tokens to individuate items of the same type (Kanwisher, 1987). Adopting this framework, Baylis and colleagues interpreted the deficit in extinction as a general difficulty the patients had in individuating items, with this problem being exacerbated when the task-relevant type information is repeated. Several subsequent studies have demonstrated the robustness of this finding (Baylis et al., 1993; Baylis, Gore, Rodriguez & Shisler, 2001; Rafal, Danziger, Grossi, Machado & Ward, 2002; Vuilleumier & Rafal, 2000).

Why should these apparently different effects of similarity and grouping arise in extinction patients? Key procedural differences between the contrasting studies may be important here. One discrepancy, originally noted by Ward et al. (1994), is that studies reporting a beneficial effect of similarity on extinction have generally required enumeration and/or localisation responses, while studies demonstrating ‘repetition blindness’ have asked patients to make

identification and localisation responses. Ward et al. (1994) proposed that unique representations do not need to be generated for successful enumeration and therefore a failure in establishing tokens is not revealed using this paradigm. Consistent with this, Vuilleumier & Rafal (2000) reported a detrimental effect of item similarity only when discrimination responses were required and not when patients made enumeration or localisation responses (Vuilleumier & Rafal, 2000). Importantly they demonstrated that, for the same group of patients, using the same stimuli, both beneficial and detrimental effects of item repetition can be elicited. Furthermore, de Haan and Rorden (2010) demonstrated that these apparently conflicting effects of repetition can coexist occurring within the same experiment when identification is required. They demonstrated repetition costs when identifying identical stimuli as well as repetition benefits when the stimuli were similar but not the same.

In addition to the effects of task, though, there may be critical differences in the nature of the stimuli that could affect performance. One critical factor may be the ease of grouping between stimuli? Grouping is known to be modulated by the proximity of the elements (Han & Humphreys, 1999). In the study of grouping effects on extinction conducted by Gilchrist et al. (1996), the beneficial effects of grouping decreased once the elements were separated by more than 2° , suggesting spatial limitations over which perceptual grouping can take place. Consistent with this, studies reporting positive effects of similarity on extinction have typically used displays with relatively proximal stimuli (e.g. each item appearing 4.8° from fixation; Ward et al., 1994). In contrast, studies reporting disruptive effects of similarity have often used widely separated stimuli (e.g. each item in a 2-item display appearing 15° from fixation; Baylis et al., 2001). Perceptual grouping is likely to be weaker (if indeed present at all) with such displays. In addition, studies showing positive effects of similarity have usually removed the fixation cross once the target stimuli onset (Gilchrist et al., 1996; Ward et al., 1994), while the fixation cross has remained present when negative effects of similarity have

been reported (e.g. Baylis et al., 1993; Baylis et al., 2001). Perceptual grouping should be stronger when there is not a separate stimulus (the cross) intervening between the to-be-grouped elements.

These contrasting display properties suggest that perceptual grouping was more likely to have occurred between the stimuli when positive effects of similarity on extinction have been reported. On the other hand, perceptual grouping was unlikely with the displays where negative similarity effects have been noted, when performance may reflect some further process such as the ease of consolidating two separate perceptual representations into working memory for report. The present study set out to test these proposals by examining whether contrasting effects of similarity could be demonstrated in the same patients by changing the stimulus conditions. I report four experiments. Experiment 1 used wide stimulus separations and left the fixation cross in the field when the target stimuli appeared (matching Baylis et al., 1993). Experiment 2 manipulated stimulus spacing, with the stimuli being presented closer together (reducing the distance from 12° in Experiment 1 to 3.4° in Experiment 2). Experiment 3 used wide stimulus separations but removed the fixation cross when the targets appeared. Experiment 4 eliminated the fixation cross and used relatively small inter-stimulus distances (as in Experiment 2). Am I able to shift performance from negative effects of similarity (in Experiment 1) to positive effects (in Experiment 4) by varying factors manipulating perceptual grouping?

General Method

Patient Summaries

AS, a male right-handed lighting technician born in 1935, suffered a right-hemisphere stroke in 2000, resulting in damage to the right inferior and middle frontal regions and medial temporal cortex. AS showed signs of extinction under bilateral stimulus condition (Soto, et al., 2009).

HB, a male linguist born 1936 suffered a right cerebral artery stroke in 2009 that affected regions of the inferior frontal, superior temporal and inferior parietal lobes on CT report. HB showed some aspects of left neglect (falling outside the cut-offs for egocentric neglect on the Apples test of neglects from the BCoS (www.BCoS.bham.ac.uk; Humphreys et al., 2011), along also with extinction when stimuli were presented for sufficient durations for HB to detect single contralesional stimuli).

MC, a male right-handed former PE teacher born in 1934 had also suffered a right hemisphere stroke leading to a pattern of neglect and extinction similar to those observed in HB.

MP, a male left-handed former tool worker born in 1947, suffered an aneurysm of the right middle cerebral artery in 1992, affecting several frontotemporal parietal regions in his right hemisphere. This included the inferior frontal gyrus, the superior temporal gyrus, the supramarginal and angular gyri and the post-central gyrus. MP presented both with neglect on the Apples test and with extinction when the stimuli appeared for durations when he could detect a single contralesional stimulus.

Previous testing demonstrated that all participants exhibited visual spatial biases, pathologically omitting items presented in the left visual field. Reconstruction of the lesions for AS, MP and MC are presented in Figure 1

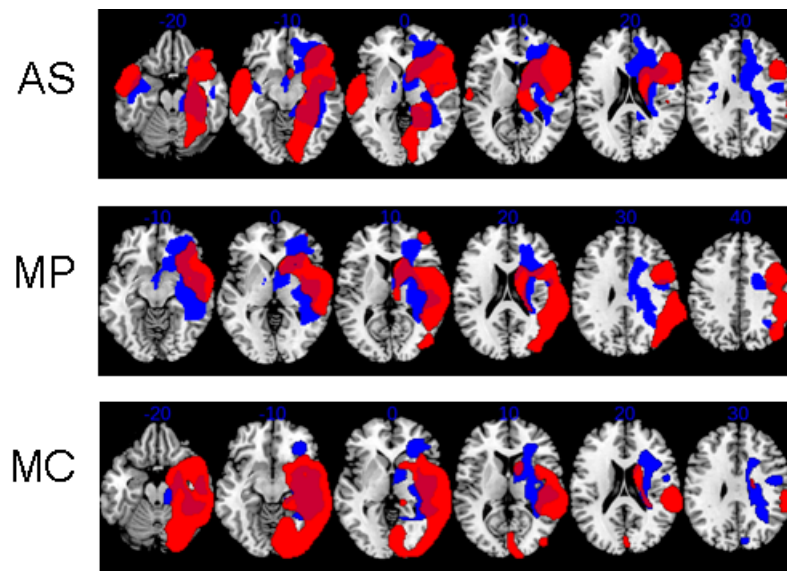


Figure 1: Lesions reconstructed from MRI scans using VBM analysis (compared to 209 controls). Significant lesion ($p < 0.001$, uncorrected) is rendered on a standard template in MRIcron where damage to gray matter is indicated in red and white in blue. The right hemisphere is displayed on the right-hand side. MRI scans could not be acquired for patient HB.

Experiment 1: Wide separations plus a fixation cross

Method

The design, stimuli and display parameters were identical to those described by Baylis and colleagues (1993).

Apparatus and Stimuli

Observers viewed the stimuli on a black display ($27^\circ \times 38^\circ$) in a darkened room with a viewing distance of 50cm. Uppercase E's and O's in red or green served as stimuli. These were presented 12° to the left and right of a white central fixation cross. Each stimulus subtended 1° high \times 0.8° wide. MatLab and psychophysics toolbox were used for all stimulus presentations and for response recording (Brainard, 1997; Pelli, 1997).

Design

In all the experiments observers took part in two tasks presented in different blocks of trials: either reporting the colour or reporting the shape of each stimulus. All blocks were preceded by both verbal and written instructions indicating the feature to be judged. Patients were instructed to point to each side of the screen responding verbally making a forced choice between the three alternative responses. For example, if taking part in the colour task patients were asked to state red, green or nothing while making their pointing response.

Each block consisted of 120 trials containing seven possible displays. This amounted to 17 trials of each condition and one extra trial selected at random from all possible display types. In all experiments two of the seven trial types were single-item displays whereby a stimulus could appear either alone, on the ipsilesional or on the contralesional side. Four of these trial-

types were two-item trials. In this case the stimuli could be identical (same shape – same colour), differ in colour only (same shape – different colour) or shape only (different shape – same colour) or differ in both shape and colour (different shape – different colour). The final display served as a catch condition where no stimulus was displayed. The order of each display type was fully randomised throughout each block.

Procedure

Before testing, all patients were familiarised with both tasks and the different display types. Practice trials of both the colour and shape task were completed to roughly titrate the stimulus duration for each participant in an attempt to avoid floor or ceiling effects. In order to satisfy this criterion the duration was kept constant within each block but differed between sessions (see Table 1). The different stimulus conditions appeared at random within a session.

	<i>Exp1</i>	<i>Exp2</i>	<i>Exp3</i>	<i>Exp4</i>
AS	700-750	650-750	550-675	400-425
HB	100	65-90	95	10
MC	800-875	550-750	875	550
MP	150	150	150	10-25

Table 1: Stimulus duration (ms) for each participant in all Experiments.

Each trial began with a white fixation cross (1.1° x 1.1°) presented in the centre of a black background. This remained present throughout the trial. Once participants reported that they were fixating on this cross and this was confirmed by experimenter observation, a ‘ready’ warning initiated the start of a trial, triggered by a keyboard press. Participants were not time-

limited in making their response following display offset. Responses were entered into the computer by the experimenter.

Results and Discussion

The mean proportions of contralesional and ipsilesional stimuli omitted on one- and two-item trials, summed across conditions, were analysed using a repeated measures ANOVA. A main effect of field was returned ($F(1,3)=20$, $p=0.021$), as significantly more left (contralesional) than right (ipsilesional) stimuli were omitted.

The proportion of contralesional stimuli omitted on two-item trials was averaged across the colour and shape-report tasks and was analysed using a paired-sample t-test across patients.

Effects of physical repetition

We examined the effects of repetition on the rate of extinction by comparing the proportion of omissions when items were identical (in both shape and colour) compared to when they were different (in both shape and colour). The data are displayed in Figure 2a. A pair-sampled t-test confirmed that significantly more omissions were made when items were identical rather than different ($t(4) = 3.42$, $p = 0.042$, two-tailed).

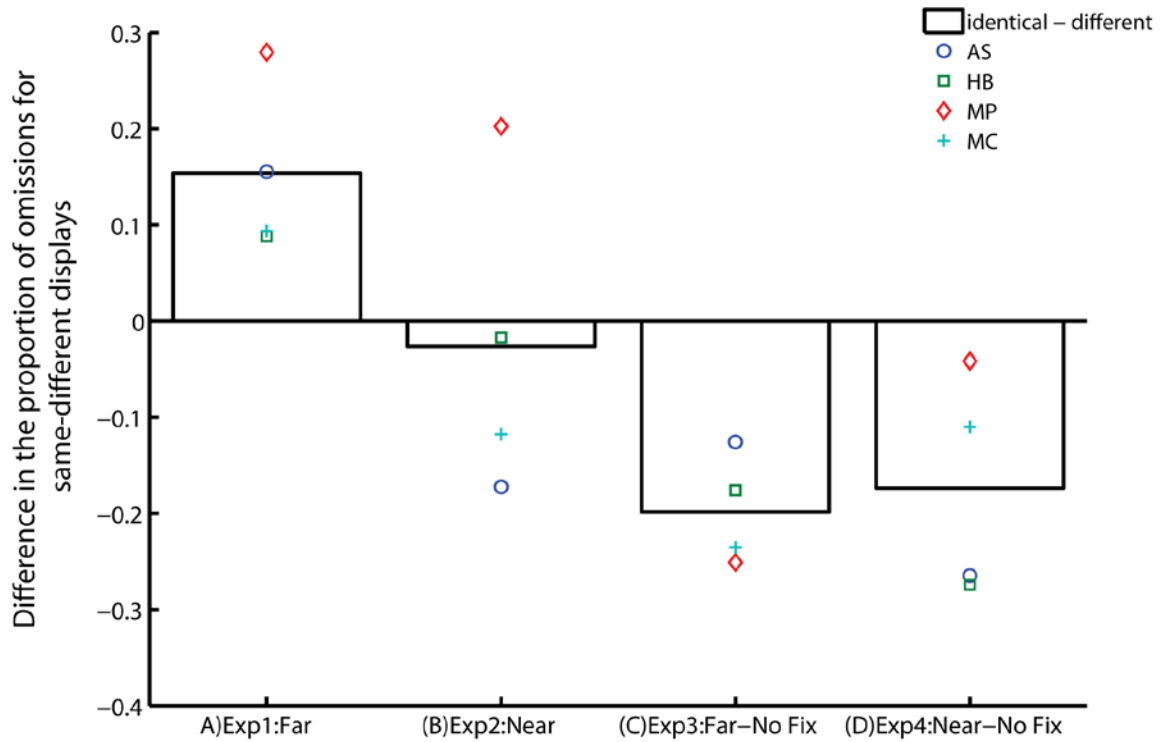


Figure 2: The mean proportion of contralesional items omitted on bilateral trials. Performance on displays with different items is subtracted from that for displays with physically identical items. Data are displayed separately along the x-axis for (A) Experiment 1, (B) Experiment 2, (C) Experiment 3 and (D) Experiment 4. Each patient is indicated with markers (AS: ○, HB: □, MP: ◇, MC: +).

Effects of repeating the task relevant feature

To isolate the effects of repeating the task relevant feature, we examined performance when this was repeated or different on two-item trials. The difference in omissions when items were identical on the relevant dimension only vs. the irrelevant dimension only was analysed. Significantly more omissions were made when the relevant dimension was repeated compared with when it differed ($t(4) = 4.64$, $p = 0.019$, two-tailed, see Figure 3a).

On the majority of two-item trials errors were due to omissions rather than incorrect responses of the wrong feature value. The proportion of erroneous feature responses did not significantly differ between conditions, although participants made more misidentification

errors when the same responses were required for both stimuli (Identical: 0.05, Relevant Repeat: 0.05, Irrelevant Repeat: 0.03, and Different: 0.02). We return to consider these errors after presenting the data for all the experiments.

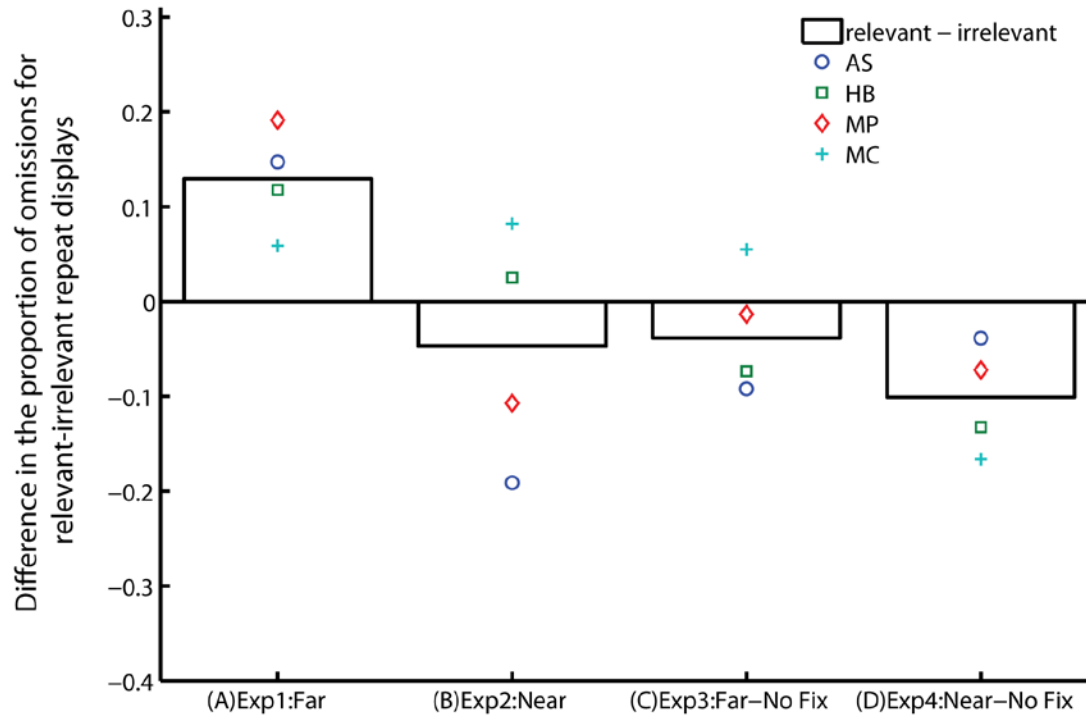


Figure 3: Mean proportion of contralesional items omitted on bilateral trials. Performance on displays with task-relevant repeating items is subtracted from that for displays with task-irrelevant repeating items.. Data are displayed separately along the x-axis for (A) Experiment 1, (B) Experiment 2, (C) Experiment 3 and (D) Experiment 4. Each patient is indicated with markers (AS: ○, HB: □, MP: ◇, MC: +).

The findings replicate those reported by Baylis et al. (1993), demonstrating detrimental effects of similarity on visual spatial biases. Like Baylis et al. I also found that these effects were modulated by the relevance of the repeated dimension, with greater extinction when response-relevant features were repeated. According to the framework outlined by Baylis et al. (1993), these findings reflect a ‘repetition blindness’ whereby an impairment in forming contralesional tokens disrupts report. This deficit is greatest when the token for the ipsilesional stimulus matches that for the contralesional item.

Experiment 2: Small separations plus a fixation cross

Method

The method was the same as in Experiment 1 except that inter-item-distance was reduced from 12° from fixation to 3.4°.

Results and Discussion

The mean proportions of contralesional and ipsilesional stimuli omitted on one- and two-item trials, summed across conditions, were analysed using a repeated measures ANOVA. These factors were field (left, contralesional / right, ipsilesional), number of items (one / two) and eccentricity (far, Exp1 / near, Exp2). The analysis returned a main effect of field ($F(1, 3) = 16.48$, $p = 0.027$); significantly more left (contralesional) items were omitted than right (ipsilesional).

Effect of physical repetition

The mean proportions of contralesional omissions on bilateral trials when stimuli were identical or different in Experiment 1 and 2 are shown in Figure 2a-b. Each patient's performance is indicated with a marker. The data were analysed using a repeated measures ANOVA including repeat (identical / all different) and eccentricity (far, Exp1 / near, Exp2) as within-subject factors. The analysis returned a significant interaction between repetition and eccentricity ($F(1, 3) = 38.09$, $p = 0.004$). There was a decrease in the cost of repetition when items were presented in close proximity. A paired-sample t-test revealed that, at a small inter-

item distance, the effect of repetition was no longer significant ($t(3) = -0.22, p = 0.838$). The proportions of errors when features were reported incorrectly were 0.03 and 0.04 in physically identical and all different conditions.

Effects of repeating the task relevant feature

Figure 2b displays the proportions of contralesional item omissions made on bilateral displays when items had only a relevant repeat vs. an irrelevant repeat. A repeated measures ANOVA returned a significant interaction between repeat (relevant / irrelevant) and eccentricity (far, Exp1 / near, Exp2) ($F(1, 4) = 13.09, p = 0.022$) reflecting a decrease in the cost of relevant repetition when items were near. Again a paired-sample t-test was used to decompose this interaction. This confirmed that the effect of relevant repetition was no longer significant when items were proximal ($t(3) = -0.82, p = 0.471$). These data indicate that altering the distance between the target stimuli reduced the negative effects of stimulus repetition on omissions. The proportions of incorrect feature reports in relevant and irrelevant repetitions were 0.05 and 0.02 respectively.

Experiment 3: Wide separations, no fixation cross

Method

The method in Experiment 3 was identical to that outlined in Experiment 1 except that the central fixation cross was offset at the onset of the target stimuli rather than being displayed throughout the trial.

Results and Discussion

The mean proportions of stimuli omitted, summed across conditions, were analysed using a repeated measures ANOVA including field (left, contralesional / right, ipsilesional), number of items (one / two) and fixation cross (present, Exp1 / absent, Exp3). Only a main effect of field was returned ($F(1, 3) = 33.75, p = 0.01$). Significantly more items were omitted in the left (contralesional) than the right (ipsilesional) visual field.

Effects of physical repetition

The proportions of contralesional items omitted on identical and different bilateral displays are displayed in Figure 2c. These data were analysed using a repeated measures ANOVA with repetition (identical / different) and fixation cross (present, Exp1 / absent, Exp3) as factors. There was a reliable interaction between repetition and the presence of the fixation cross ($F(1, 3) = 18.950, p = 0.012$). When the fixation cross was removed, there was a positive effect of stimulus similarity on report (identical > different; $t(3) = -6.8, p = 0.007$). The proportions of incorrect feature reports were 0.05 in same identity and 0.01 in the all different conditions.

Effects of repeating the task relevant feature

Figure 3c illustrates the proportions of contralesional omissions made on bilateral displays when there was a relevant or irrelevant repetition across items. The data are displayed for both Experiment 3 and Experiment 1 for comparison. A repeated measured ANOVA revealed significant main effect of repeat (relevant / irrelevant) ($F(1, 4) = 9.96, p = 0.034$), indicating that participants made more omissions when there was a repetition of the relevant feature, but this factor interacted with fixation (present, Exp1 / absent, Exp3) ($F(1, 4) = 13.02, p = 0.023$). A t-test on the data with the fixation cross removed showed that the effect of relevant repetition was now not reliable ($t(3) = -1.27, p = 0.295$). The proportions of incorrect feature responses were 0.06 and 0.01 for the relevant repeat and relevant different conditions.¹

¹ Experiment 3 was replicated with one participant (AS) whilst recording eye-movements. In this case, trials began only once AS central fixation was stable (did not exceed a velocity threshold of 30 °/sec, an acceleration threshold of 8000 degrees/sec/sec, or a motion threshold of 0.1° and the pupil was not missing for more three or more samples in a sequence). The data were compared to the results without eye-movement tracking using a loglinear analysis including Experiment (eye-tracking / not eye-tracking). Considering the effect of repetition, a model was returned retaining all factors ($X^2(3) = 0.919, p = 0.821$) which indicated that accuracy interacted with repetition ($X^2(1) = 4.242, p = 0.039$), but not with Experiment ($X^2(1) = 0.829, p = 0.363$). Considering the effect of repetition relevance, a two-way model was returned retaining accuracy and experiment ($X^2(5) = 3.825, p = 0.575$). Neither repetition nor experiment interacted with accuracy. Thus the results held even when we ensured that fixation remained.

Experiment 4: Small separations no fixation cross

Method

The method in Experiment 4 was identical to that outlined in Experiment 2 except that the central fixation cross was offset on stimulus onset rather than being displayed throughout the trial.

Results and Discussion

The mean proportions of stimuli omitted, summed across conditions, were analysed using a repeated measures ANOVA including field (left, contralesional / right, ipsilesional), number of items (one / two) and display (far fixation, Exp1 / near no fixation, Exp4). This analysis returned a main effect of field only ($F(1, 3) = 19.09$, $p = 0.022$); significantly more items were omitted in the left (contralesional) than right (ipsilesional) visual field.

Effects of physical repetition

Figure 2 displays the proportion of contralesional items omitted from bilateral displays according to whether the stimuli were identical or different. The data were analysed using a repeated measures ANOVA with the factors being repetition (identical / different) and display (far fixation, Exp1 / near no fixation, Exp4). There was a significant interaction between repetition and display ($F(1, 4) = 38.24$, $p = 0.003$). When the items were closely spaced and there was no fixation, there was a trend for similarity to facilitate performance ($t(3) = -2.97$, p

= 0.059). The proportions of erroneous responses were 0.05 and 0.01 in the repeat and all different conditions.

Effects of repeating the task relevant factors

Figure 3d illustrates the proportions of contralesional item omissions on bilateral trials when there was a task-relevant or irrelevant repetition across items. A repeated measured ANOVA revealed a significant interaction between repeat (relevant / irrelevant) and display (far fixation, Exp1 / near no fixation, Exp4) ($F(1, 4) = 10.12, p = 0.034$). When the items were proximal and fixation cross was absent, relevant repetition facilitated performance ($t(3) = -3.48, p = 0.04$). The proportions of incorrect responses were 0.12 and 0.01 for the relevant vs. irrelevant feature conditions.

Across-Experiment Comparison

To confirm the overall changes in performance across the conditions, overall across-experiment comparisons were made on the omission data on two-item trials. For the effect of exact repetition (features all the same vs. different) there was an overall interaction between repetition and experiment ($F(3, 9) = 10.07, p = 0.003$). A similar borderline interaction occurred for the effects of task relevant repetition ($F(3, 9) = 5.84, p = 0.087$, greenhouse geisser corrected). These ANOVAs confirm that the effects of physical and task-specific repetition changed as a function of the display conditions.

A similar overall analysis was performed on the data for the effects on the report of incorrect features. For the contrast between exact repeat vs. all different trials there was a similar interaction between experiment and repetition ($F(3, 9) = 4.19, p = 0.041$). The proportion of incorrect feature errors changed as a function of the display characteristics. In Experiment 1, 3 and 4 patients tended to make more errors when the stimuli required the same response. However, in Experiment 2, when items were proximal and the fixation cross was present, participants tended to make more incorrect responses when stimuli required a different response i.e. they incorrectly responded that items had the same target feature when they did not (though this effect was not reliable). In all Experiments however the proportion of incorrect responses did not differ between conditions. The contrast between task relevant repeat and different trials did not return any reliable effects or interactions. Unlike omissions, feature errors occurred on a relatively small proportion of trials (0.06 vs. 0.04) and they may generally reflect a bias against reporting features of contralesional items as being the same as those of the ipsilesional item. Such a bias would generate more errors on repetition trials than on trials where the features of the stimuli differ.

Discussion

These experiments demonstrate that performance can be shifted from negative to positive effects of stimulus similarity on extinction (omission errors under two-item conditions), dependent on the presentation conditions. Under conditions favourable to perceptual grouping (with small separations between stimuli, with the fixation cross removed when the targets onset), there was a beneficial effect of exact repetition (fewer omissions on repeat than different trials). Interestingly, under these conditions there were either no effects of repeating task-relevant over task irrelevant features or task-relevant repetition improved performance (Experiment 4). Under conditions discouraging grouping (with wide separations and with the fixation cross maintained throughout the trial), there was a negative effect of both exact repetition and the repetition of task-relevant features. The former results replicate one set of prior findings in the literature (Gilchrist et al., 1996; Humphreys, 1998; Pavlovskaya et al., 2000; Pavlovskaya et al., 1997; Ward et al., 1994) while the latter replicate another (Baylis et al., 1993; Baylis et al., 2001; Rafal et al., 2002; Vuilleumier & Rafal, 2000). The data show that both sets of findings can occur, depending on the display conditions, and that a likely critical factor is the extent to which the ipsi- and contralesional stimuli form a single perceptual group vs. the extent to which they are identified as separate perceptual objects. Similarity benefits the first process and disrupts the second.

These findings highlight an important difference between ‘repetition blindness’ and similarity grouping. Unlike ‘repetition blindness’, similarity grouping was not necessarily modulated by the response relevance of the repeated feature, and beneficial effects of grouping are seen primarily when items are identical in both shape and colour (see especially Experiment 3). This is consistent with the idea that grouping operates at an early pre-attentive processing stage to organise visual information for subsequent attentive processing. Evidence in support

of this claims comes from studies showing that grouping can operate even in the apparent absence of selective attention (Kimchi & Razpurker-Apfeld, 2004; Lamy, Segal, & Ruderman, 2006; Moore & Egeth, 1997) and is associated with neuronal activity in early regions of the occipital and temporal cortices, specifically including the calcarine cortex (Han, Ding, & Song, 2002). Moreover, Pavlovskaya et al. (1997, 2000) have presented evidence suggesting that the processing of two distal elements as a single object is subserved by long-range lateral interactions in early visual processing stages outside the parietal lobes, which are frequently damaged in extinction patients (Pavlovskaya et al., 2000; Pavlovskaya et al., 1997). I reason therefore that the positive effects of grouping on extinction reported here are driven by low-level grouping processes that are sensitive to the display structure. These effects differ importantly from the detrimental effects of repetition, which are strongly influenced by task relevance. This latter result suggests that ‘repetition blindness’ occurs at later stage in processing, modulated by top-down prioritisation for task-relevant features. For example, ‘repetition blindness’ may occur at a stage in which separate tokens are entered into visual short-term memory. If the patients have difficulty forming stable tokens of items on the contralesional side (e.g. due to poor localisation coding, see Baylis et al. 2001), then they may have more difficulty in registering a repeat of the critical feature than when the critical feature changes. ‘Extinction’ then takes place (see Riddoch et al., 2010).

One other potential factor that can influence performance when items are repeated is response bias (Fagot & Pashler, 1995). In conditions of uncertainty, participants may be reluctant to make the same response twice. The results with feature misidentifications are consistent with this: participants tended to make more feature identification errors in the relevant response conditions, compared to the conditions with different features. These ‘different feature reports’ also arose on a small proportion of single item (ipsilesional) trials, consistent with them reflecting a response bias. If anything, the response bias would inflate performance in

the non-repeat conditions, running counter to the positive effect of perceptual grouping observed. The fact that positive effects of grouping occurred under critical conditions (small separations, fixation cross removed), however, indicates that a response bias was unlikely to be causative of the changes in omission errors observed.

The current study demonstrates that despite the processing deficits in neglect and extinction, grouping is intact and here modulated the severity of visual-spatial biases. These findings are consistent with previous reports of beneficial effects of low-level grouping mediating stimulus detection (Gilchrist et al., 1996; Ward et al., 1994) and extend this further to include improvements in feature identification when stimuli are proximal and not separated by other intervening items (e.g. a fixation cross). Under contrasting conditions, when items are presented at wide eccentricities and separated by a central fixation cross, stimuli may be selected consecutively and give rise to individuation difficulties in patients. Similarity can both help and hurt selection according to the display conditions.

CHAPTER 3

THE GROUPING BENEFIT IN EXTINCTION: OVERCOMING THE TEMPORAL ORDER BIAS

Synopsis

Grouping between contra- and ipsilesional stimuli can alleviate the lateralised bias in spatial extinction (Gilchrist, Humphreys, & Riddoch, 1996; Ward, Goodrich, & Driver, 1994, Chapter 2). In the current study I demonstrate for the first time that perceptual grouping can also modulate the spatio/temporal biases in temporal order judgements affecting the temporal as well as the spatial coding of stimuli. Perceived temporal order was assessed by presenting two coloured letter stimuli in either hemi-field temporally segregated by a range of onset-intervals. Items were either identical (grouping condition) or differed in both shape and colour (non-grouping condition). Observers were required to indicate which item appeared second. Patients with visual extinction had a bias against the contralesional item appearing first, but this was modulated by perceptual grouping. When both items were identical in shape and colour the temporal bias against reporting the contralesional item was reduced. The results suggest that grouping can alter the coding of temporal relations between stimuli.

Introduction

In Chapter 2 I discussed that following unilateral brain damage patients can show spatial biases in visual processing. This can manifest in visual extinction, characterised by successful detection of a single stimulus presented in either hemi-field but failures to detect contralesional events that are accompanied by an ipsilesional stimulus (Karnath, 1988). In addition to poor report of the presence of contralesional stimuli, there is also evidence that temporal processing can be impaired in patients showing spatial biases (Di Pellegrino, Basso, & Frassinetti, 1998; Mavritsaki, Heinke, Deco, & Humphreys, 2009; Rorden, Mattingley, Karnath, & Driver, 1997). Rorden et al. (1997) examined the perception of temporal order in patients showing visual extinction. Two bilaterally presented bars were segregated by a range of temporal intervals and patients had to report which bar appeared first. In marked contrast to control participants, patients with extinction consistently reported ipsilesional events as occurring sooner than physically simultaneous contralesional events. Bilateral items were judged to be synchronous only when there was a substantial lead for the contralesional item (approximately 200ms in this study).

Rorden et al. (1997) proposed that the primary deficit in extinction was a bias in orientating spatial attention and that this could have secondary effects on temporal processing. According to the law of 'prior-entry', attended items will be perceived as appearing sooner than those which are synchronous but unattended. This has been confirmed for normal visual observers, who report that attended items appear before physically simultaneous but unattended items (Stelmach & Herdman, 1991). Accordingly, chronic allocation of attention to ipsilesional stimuli will lead to positive biases in judging their onset compared to that of contralesional stimuli. Temporal biases in processing across the visual field have also been reported in studies of extinction. Cate and Behrmann (Cate & Behrmann, 2002) and Rorden et al.

(Rorden, Jelsone, Simon-Dack, Baylis, & Baylis, 2009), for example, both reported greater extinction with temporally segregated displays when the ipsilesional stimulus leads the contralesional, consistent with faster engagement of attention on the ipsilesional stimulus and poor item disengagement. In Cate and Behrmann's (2002) study, this effect occurred even when both stimuli fell in the ipsilesional field, suggesting processing biases exist across space.

Here I assessed, for the first time, whether biases in temporal perception in patients showing spatial extinction could be ameliorated by grouping. As discussed in the previous two chapters, grouping refers to the process organising our perception from unstructured parts into coherent wholes. Studies of spatial extinction have demonstrated that grouping can affect spatial biases in stimulus report (Ward et al., 1994; Gichrist et al., 1996, and Chapter 2 here). Conditions that promote perceptual integration of distal items into a single object reduce an otherwise pathological bias in the competition for attention, allowing both items to be selected together.

Rorden et al. (1997) have considered the possibility that grouping could influence temporal order perception in extinction patients. They assessed the 'line-motion illusion', in which observers appear to perceive movement in a horizontal bar from an attended to an unattended location (Hikosaka, Miyauchi, & Shimojo, 1993). Given pathological attention to the ipsilesional side, one might expect extinction patients to be biased to seeing the bar move from the ipsi- to the contralesional side. However, Rorden et al. failed to find such a bias. They suggested that the bias may be modulated by the bar forming a single global object linking the contra- and ipsilesional sides (though direct evidence for grouping was not presented). Interestingly, grouping effects have been found on temporal order judgments with normal participants. Specifically, temporal asynchrony between stimuli has been shown to be

more difficult to judge when visual stimuli group (Nicol & Shore, 2007), suggesting that detection of physical differences in temporal onsets can be overridden by grouping. The effects of grouping on subjective asynchrony however have not been examined. I tested if spatial biases in temporal order judgements were overridden by colour and shape grouping in three patients suffering from extinction following brain damage. To vary grouping, the stimuli either had the same colour and shape or differed in both properties. Prior evidence suggests that there should be stronger grouping for the same colour-shape items than for the items that differ in these properties (Kubovy, Cohen, & Hollier, 1999).

Method

Participants

AS, a male right-handed lighting technician born in October 1935 suffered a right-hemisphere stroke in 2000 causing lesions to the right inferior and middle frontal regions and medial temporal cortex.

DB, a right-handed male chef born in October 1935, suffered a left-hemisphere stroke in 1994 that resulted in damage to the left temporal and parietal cortices.

RH, a male left-handed plumber born in October 1933 suffered a stroke in 1999 that affected several regions in the left-hemisphere: inferior parietal and superior temporal lobes, including the angular gyrus.

The patients' lesions are presented in Figure 4. All the patients suffered their lesion at least 9 years pre-testing and they were all in a stable state.

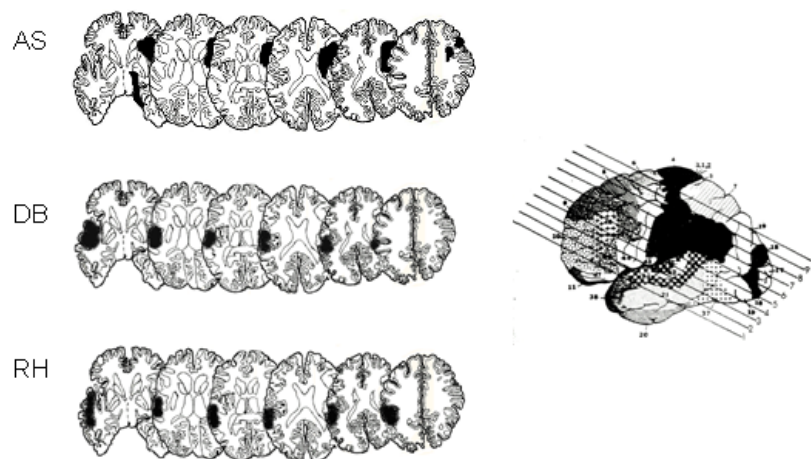


Figure 4: Reconstruction of patients' lesions from MRI scans. Lesions have been drawn onto standard slices from Gado et al. (Gado, Hanaway, & Frank, 1979). The right hemisphere is shown on the right. The right figure shows the 10 slices used. Only slices 3 – 8 are depicted.

Extinction was demonstrated in an initial set of trials. Participants were asked to identify briefly presented green or red letters (E or O, 1° high x 0.8° wide) presented to 3.5° the left and / or right of fixation. Stimulus durations were titrated across consecutive series of 40 trials to ensure that performance on unilateral contralesional stimuli displays was around 70% in one block. Table 2 presents the results for unilateral and bilateral presentation trials averaged over the report of identity and colour. There was clear evidence of extinction, with worse performance on bilateral than unilateral trials for each patient. Errors on bilateral trials reflected poor report of the contralesional stimulus in each case. There was also some evidence of impairments on unilateral trials, and control participants perform at ceiling with both unilateral and bilateral presentations at the durations used. Nevertheless, the drop in performance on bilateral relative to unilateral trials is consistent with extinction operating at the present exposures.

Table 2: Percentage of contralesional stimuli correctly identified when presented in isolation (unilateral) and simultaneously with an ipsilesional item (bilateral) at the stimulus duration specified. The PSS (point of subject simultaneity) and JND (just noticeable difference) for each patient in grouping and non-grouping experimental conditions are displayed in the last four columns.

Patient	Stimulus Duration (ms)	Unilateral (%)	Bilateral (%)	<i>PSS (ms)</i>		<i>JND (ms)</i>	
				<i>Grouping</i>	<i>Non - Grouping</i>	<i>Grouping</i>	<i>Non - Grouping</i>
AS	300	75	6.75	14.11	37.02	67.56	58.98
DB	175	75	37.5	50.78	77.81	41.68	36.29
RH	300	62.5	6.75	50.14	103.91	121.74	119.81

Three self-reported neurologically healthy right-handed control participants approximately age-matched to the patient participants also took part. BD a female born in 1940, BN a male born in 1937 and KN a female born in 1934. Control participants completed the experiment in one day of testing and were paid for their participation.

Apparatus and Stimuli

Participants viewed stimuli on a black display ($27^\circ \times 38^\circ$) in a darkened room. The computer monitor was adjusted to ensure observers were positioned centrally at a distance of approximately 50cm. Stimuli were uppercase E's and O's in Arial font coloured in red or green that subtended a visual angle 1° high \times 0.8° wide. The stimuli were positioned 3.5° to the left and right of a white central fixation point ($1^\circ \times 1^\circ$). Stimulus presentation and response collection was controlled using MatLab with the psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Design

Experimental testing sessions consisted of two blocks of temporal order judgement trials, each consisting of eighty-eight trials with bilateral stimulus displays. I employed a 2×2 factorial design, systematically manipulating grouping between contra and ipsilesional items, and the difference in their temporal onsets. On half of the trials the stimuli were identical whilst on the other half they differed in both shape and colour. Each trial type was presented at eleven different temporal intervals (SOA): one synchronous presentation and ten asynchronous onsets. In accordance with the method outlined by Baylis et al. (Baylis, Simon, Baylis, & Rorden, 2002), asynchronies were varied systematically and were a proportion of the stimulus duration set for each patient. The proportions were: 0.1 x, 0.25 x, 0.5 x, 0.8 x, and 1.0 x stimulus duration. On half of the asynchronous displays the ipsilesional item came

first (negative SOAs) and on half the contralesional item was presented first (positive SOAs). Within each block, both trials with identical and different stimuli were presented at each temporal interval four times. The order of stimulus presentation was fully randomised for each participant.

Procedure

Before experimental testing, participants were familiarised with the task and display procedure in a practice session. Participants were required to point to the item that appeared second. They were told that the items would always be asynchronous (despite synchrony on 9% of trials) and that they should guess if uncertain of the correct response. Responses were not time-pressured and participants were encouraged to be as accurate as possible. Instructions were reiterated in oral and written form directly prior to each block of experimental testing.

Each trial began with a white cross presented centrally on a black display. Participants verbally reported when they were fixating on this point; this was then confirmed by experimenter observation. A verbal 'ready' warning followed to initiate the trial start that was triggered by a keyboard press. The central fixation cross was offset on trial onset. Stimuli were presented at variable temporal intervals and remained on screen until a response was given. Participants were given an unlimited time to respond. The response was entered into the computer by the experimenter. All participants completed eight testing sessions of two blocks each (64 trials per condition). For the patients this was conducted over weekly intervals between October 2009 and February 2010. Performance was stable across this time period.

Results

The mean performance of all patients and age-matched control participants is shown in Figure 5. The data are represented as the proportion of ‘ipsilesional item second’ responses, which are plotted as a function of SOA. Temporal asynchronies are expressed as a proportion of the stimulus duration. Psychometric performance was fitted with a Weibull function using *psignifit* v. 2.5.6 (<http://bootstrap-software.org/psignifit/>), which implements a maximum-likelihood method (Wichmann & Hill, 1991). Error-bars were calculated on the fits from 4999 bootstrap replications of the data.

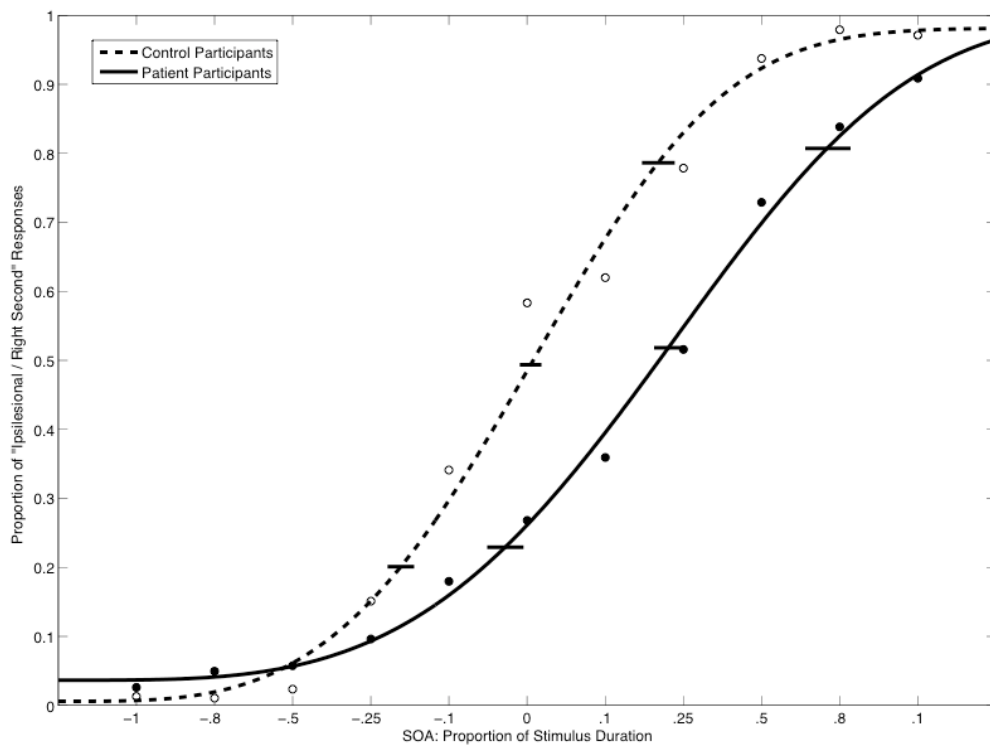


Figure 5: Mean proportion of ipsilesional / right item second responses is shown for patient (filled circles) and control (open circles) participants. This is plotted as a function of temporal asynchrony, which is expressed as a proportion of the stimulus duration used to elicit extinction. Negative values (to the left) indicate a lead for the ipsilesional stimulus, and positive values (to the right) reflect a contralesional stimulus on-setting before an ipsilesional. Larger values reflect greater differences in temporal onsets.

Inspection of Figure 5 reveals that, in contrast to the age-matched control observers, the perception of simultaneity in patients with extinction did not correspond with synchronous presentation. The psychometric function of the patients was shifted rightwards indicating a bias in perceiving the contralesional item as on-setting later than the ipsilesional one. On average, the ipsilesional item had to appear nearly 35ms later than the contralesional stimulus in order to perceive them as simultaneous.

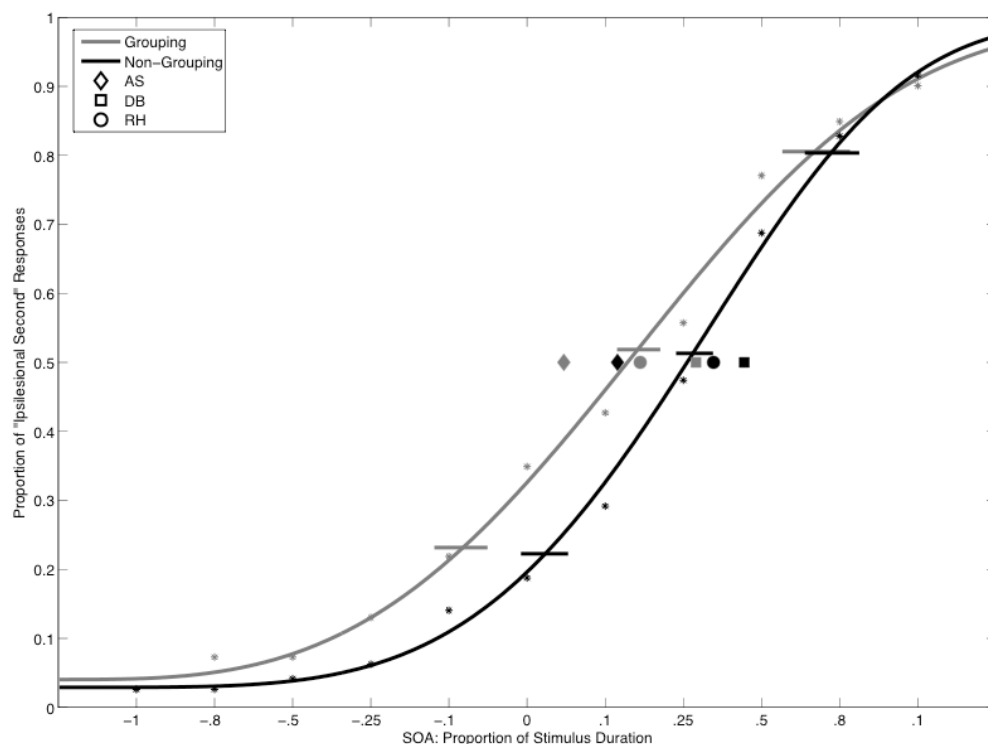


Figure 6: Mean proportion of ipsilesional item second responses is indicated with an asterisk (*) and plotted separately for each experimental condition as a function of stimulus onset asynchrony. Psychometric functions have been fitted to these data are displayed along with each patients PSS threshold.

To examine whether this delay was affected by our grouping manipulation psychometric functions for each experimental condition were fitted. Figure 6 shows that the rightward shift in the temporal discrimination function was greater when items differed in shape and colour than when they were identical. To quantify psychometric performance in each condition the thresholds at the point of subjective simultaneity (PSS) were extracted and the 'just noticeable difference' (JND) calculated. The PSS is the point at which the fitted sigmoid curve reached

0.5 (i.e. chance), corresponding to when ipsilesional and contralesional items were judged to be second equally often. The PSS for each patient was calculated separately and the data are indicated in Figure 6. The JND indicates the smallest temporal interval required for participants to reliably judge which item was second and this was calculated by finding the difference between the function values for 25% and 75% ipsilesional-second responses and dividing by two. These measures were extracted for each patient for each experimental condition.

The resulting PSS and JND are detailed in Table 2. These data were entered into a paired t-test. When the items were identical in both shape and colour the PSS was significantly smaller ($t(2) = -3.574$, $p = 0.035$) than when they differed. Consistent with this, the error-bars (95% confidence intervals) of the functions for each of the experimental conditions do not overlap at the PSS. There was also a borderline effect of grouping on JNDs, with JNDs tending to increase when items were identical ($t(2) = 2.755$, $p = 0.055$ n.s). The slope of the temporal discrimination function tended to be shallower when items grouped.

Discussion

Consistent with previous reports (Di Pellegrino, et al., 1998; Rorden, et al., 1997), the data presented here demonstrate that temporal processing is impaired in patients with extinction and that items presented in the contralesional hemi-field are perceived as appearing later than those in the ipsilesional hemi-field. Importantly, the magnitude of this delay was reduced when the contralesional and ipsilesional stimuli were grouped on the basis of low-level perceptual features (here matching both colour and shape). A smaller contralesional temporal lead was therefore required for extinction patients to perceive the two identical items as occurring simultaneously than two items differing in both colour and shape.

These findings corroborate previously reported beneficial effects of inter-item grouping on extinction (Gilchrist, et al., 1996; Ward, et al., 1994; Chapter 2 here). Grouping improves contralesional item detection, and these findings extend this to incorporate effects on temporal processing when judging order. I now consider whether these findings can be reconciled within the current understanding of the temporal processing bias in extinction and the effect of grouping on this deficit, and conclude by offering an alternative explanation.

A common explanation for the beneficial effects of grouping on extinction is that the selection weight of pathologically disadvantaged contralesional items is rebalanced by a process by ‘weight-linkage’ ensuring that both stimuli are selected simultaneously (Gilchrist, et al., 1996; Ward, et al., 1994). In this way, grouping can overcome the biased spatial gradient rebalancing the allocation of attention. Rorden et al. (1997) argued that temporal processing impairments are a consequence of biased spatial orienting, which speeds processing of attended stimuli relative to stimuli that are physically synchronous but unattended. According to this reasoning, by redressing spatial imbalances in attention by grouping, any temporal

impairment is reduced and the processing time-course proceeds normally. A key assumption of this explanation is that temporal processing arises as a consequence of impaired orientating of spatial attention and is indirectly modulated by grouping.

There is however evidence that the temporal order bias in extinction is independent of the spatial deficit (Cate & Behrmann, 2002; Husain, Shapiro, Martin, & Kennard, 1997). Within this framework, a somewhat different account is required that does not rely on grouping indirectly modulating a spatial orientating impairment. Observations that temporal order perception judgements of neurologically healthy participants are directly influenced by grouping would support an alternative account (Nicol & Shore 2007). Participants' ability to judge asynchrony between two visual events is compromised when the items group based on object completion or low-level features, compared with when they do not group. For items which group, the slope of the temporal discrimination function is shallow, as the relative onsets of the two events are more difficult to judge. Analogous findings have been robustly reported cross-modally in conditions where stimuli are highly consistent based on low-level and/or high-level factors (Calvert, Spence, & Stein, 2004). It may be that unified stimuli are 'yoked' together altering the coding of temporal relations between items (Keetels & Vroomen, 2005; Vatakis & Spence, 2007). The effect of grouping on subjective asynchrony reported in our study is strikingly similar to that seen when normal individuals resolve physical asynchrony and may be attributable to a similar mechanism. This explanation differs importantly from the spatial orienting account as grouping directly affects the temporal processing bias.

The current data indicate that grouping can take place despite the processing deficits apparent in extinction patients. In the present case, grouping between contra- and ipsilesional events leads to a reduced bias in temporal judgements of which item came second.

Part 2: Binding of learned features

CHAPTER 4

DISRUPTIVE EFFECTS OF DIAGNOSTIC COLOUR AT DIFFERENT LEVELS OF PROCESSING: EVIDENCE FOR THE AUTOMATIC LINKAGE OF COLOUR-SHAPE OBJECT REPRESENTATIONS

Synopsis

I examined the effects of surface colour on object identification by testing whether colour-shape associations can interfere with as well as facilitate identification. I used colour-diagnostic objects rendered in either typical or atypical colours, which appeared either on an item's surface or its surround. On a majority of trials participants had to name the objects. However, when the colour red appeared, participants were asked to name the hue rather than the object. Object naming was faster when the stimuli were correctly coloured relative to when they were coloured incorrectly. In contrast, response times to respond 'red' were slowed when objects appeared in their diagnostic colour. With unlimited exposures this interference effect on colour naming was equally large when the colour fell in the background and when it appeared on the object's surface. With limited exposure durations, interference was found only when the colour appeared on an objects surface. The data indicate that, under short exposures, interference reflects access to perceptual representations of objects that code surface colour as well as form. With long exposures there can also be interference from the joint activation of object identity and colour properties in semantic memory, which occurs for surface and background colour alike.

Introduction

Our successful and efficient recognition of objects within a complex and dynamic environment is a remarkable ability of our visual system. The mechanism by which this is achieved has been the subject of extensive research. In this chapter I specifically focus on the integration of colour-and-shape within object recognition.

Early, and still influential, ‘edge-based’ theories of object recognition emphasise the importance of object form in identification (Biederman, 1987; Grossberg & Mingolla, 1985). One leading edge-based account is ‘recognition by components’ proposed by Biederman (1987) that assumes recognition is achieved by a decomposition of objects into simple volumetric components, ‘geons’. Objects are therefore understood to be represented as an arrangement of these primitives. Clearly form is important in object recognition but whether this is sole basis for identification has been contentious. Recently strict ‘edge-based’ theories have been revised to allocate a role for surface information to facilitate recognition when visual input is degraded by viewing conditions (Nicholson & Humphrey, 2001; Wurm, Legge, Isenberg, & Luebker, 1993) or following brain injury (Mapelli & Behrmann, 1997). Within this framework colour does not form part of a visual object representation and is allocated a role only at a late stage of object processing. It is this latter point that distinguishes ‘edge-based’ theories from ‘surface-plus-edge’ accounts, which by contrast argue that representations contain multiple features of an object including both form and surface information even at the earliest stage of perception (Davidoff, 2001; Tanaka, Weiskopf, & Williams, 2001).

Contrasting accounts have been tested by examining whether object recognition and naming is facilitated by the presence of appropriate colour surface information but these

experiments have yielded mixed results. Studies have reported faster recognition of objects that are appropriately coloured (e.g. yellow banana) rather than inappropriately coloured (e.g. blue banana) or gray-scale depictions (Price & Humphreys, 1989; Tanaka & Presnell, 1999; Wurm et al., 1993). And seemingly contrary studies have reported that recognition is unaffected by the colouring of an object (Biederman & Ju, 1988). Achromatic line-drawings of common objects can be verified as quickly as coloured versions (Biederman & Ju, 1988). Similarly adding realistic colour to photographs of objects did not improve performance relative to the grey-scale version (Ostergaard & Davidoff, 1985). Methodological differences may be important in understanding the apparent discrepancy. Evidence suggestive of an achromatic mental representation has been criticised based on stimuli. Ostergaard and Davidoff's sample set was very small (maximum 4 items) and therefore may not have been a sufficiently powerful design to observe any reliable effects of colour. Biederman and Ju (1988) used a larger set of 29 items, however most were metallic (e.g. classic telephone) or achromatic (e.g. fork) and only five had an associated colour (e.g. banana). Furthermore line drawings are simplified depictions of an object emphasising key edges, how these are processed may tell us very little about natural object processing

'Colour-diagnostics' may be particularly important in determining whether colour facilitates recognition. This is the degree to which shape and colour are consistent and have a learned relationship, for example yellow is highly diagnostic of a banana but not of a bicycle (Tanaka et al., 2001). As noted, of the 29 stimuli used by Biederman and Ju (1988), only 5 had a 'natural' (i.e. diagnostic) colour. This explanation does not however tell us *why* recognition of diagnostic items is aided by colour surface information. This is critical for distinguishing between theories of object recognition because although there is an overall consensus that recognition of diagnostic objects could be facilitated by appropriate

colouring only ‘surface-plus-edge’ theories argue that colour and shape are intertwined in the objects representation.

One study has attempted to address the critical question of whether the diagnostic colour and shape of an item are intrinsically bound. Naor-Raz and colleagues (2003) had participants name the colour of objects and found faster response latencies when the colour was correct for the object relative to when it was incorrect (see also Ménard-Buteau & Cavanagh, 1984). They proposed that object identity and name information could be automatically activated. When the identity and name information is compatible with the colour, colour naming benefits relative to when identity, name and colour information is incompatible. However, given that object identity and name information had a 50% probability of being compatible with the colour, it is possible that participants deliberately processed the objects to facilitate colour-naming performance. Facilitation as a measure of automaticity may therefore not be ideal here. In addition, the relations between the object interference effects and the grouping of object and colour information was not examined; are the object interference effects contingent on the objects and colours being coded in an integrated fashion? Or, do the effects reflect activation of learned shape and colour properties at a semantic level, when integrated representations may not be critical?

The present study examined these two issues. I had participants undertake two tasks. Objects depicted in any colour but red had to be named (e.g. yellow banana, participants respond ‘banana’). However, if the colour red was presented, participants had to name the colour not the object (e.g. red strawberry, participants respond ‘red’). Since on ‘red’ trials the object’s identity and name were never relevant to the task, then identity and name information should not be used deliberately. I examined trials when colour and the object were compatible (when the correct colour was shown for the object) and when they were

incompatible (the colour was not correct for the object). On object naming trials, responses should be faster for the object depicted in a compatible relative to incompatible colour consistent with the correct colour information facilitating object identification (Joseph, 1997; Joseph & Proffitt, 1996; Nagai & Yokosawa, 2003; Ménard-Buteau & Cavanagh, 1984; Naor-Raz, et al., 2003; Nicholson & Humphrey, 2001; Price & Humphreys, 1989; Tanaka & Presnell, 1999; Wurm, Legge, Isenberg, & Luebker, 1993). In contrast, on colour-naming trials (respond 'red'), a compatible object may disrupt performance because the enhanced identification response would compete with the colour name. In this way automatic integration of associated colour and shape would be indexed by interference. Further, this would be the first demonstration that the correct colour-object association can disrupt colour naming performance.

In addition to varying whether objects were correctly or incorrectly coloured, a second critical manipulation was to vary whether the depicted colour fell on the surface of the objects relative to when it fell in the background. Studies of object naming have shown that the benefits of depicting stimuli in the correct colour are increased when the colour is presented on an object's surface rather than the background (Prevor & Diamond, 2005; Price & Humphreys, 1989). Here I assess for the first time whether the same holds for interference effects from objects on colour naming. Note that interference effects on colour naming could emerge in a number of ways. One is if there is stronger activation of a stored perceptual representation for the object when it is correctly relatively to incorrectly coloured. The strongly activated perceptual representation may in turn lead to strong activation of the object's name, generating competition for the naming response. This perceptual representation may be sensitive to the familiar visual appearance of the stimulus, and so be activated more when the colour is on the surface of the object rather than the background. A second possibility is that there is competition at the level of name

retrieval from the strong activation of a semantic representation of the object, when colour information is correct rather than incorrect. I presume that a semantic, as opposed to a perceptual, representation of a stimulus will be less sensitive to the presence of the colour on the surface of the object rather than the background, to the extent that semantic representations list stimulus properties across different modalities and perceptual instantiations (e.g., Humphreys & Forde, 2001). To activate such representations, it may be sufficient for both shape and colour properties to be present. However, since perceptual representations should be activated earlier in time than semantic representations, then interference deriving from the perceptual representations of objects may be more evident under limited exposure conditions.

I report four experiments. In Experiment 1, the stimuli were presented for unlimited durations. In Experiment 2, I used limited exposures. In Experiment 3, I again used brief stimulus exposures, but now with the backgrounds rather than objects being fixated – this was done to ensure that any reduced effects of background colour, in Experiment 2, did not reflect limitations on processing peripheral colours when stimulus exposures were reduced. In Experiment 4 I ran a control experiment where participants engaged in a colour-naming task only.

Experiment 1: Unlimited Exposure

Method

Participants

Twenty-four undergraduate and postgraduate students at the University of Birmingham participated in exchange for course credits (18-27, 8 male, 3 left-handed). All participants reported normal / corrected acuity, normal colour vision, and spoke the English language fluently.

Stimuli

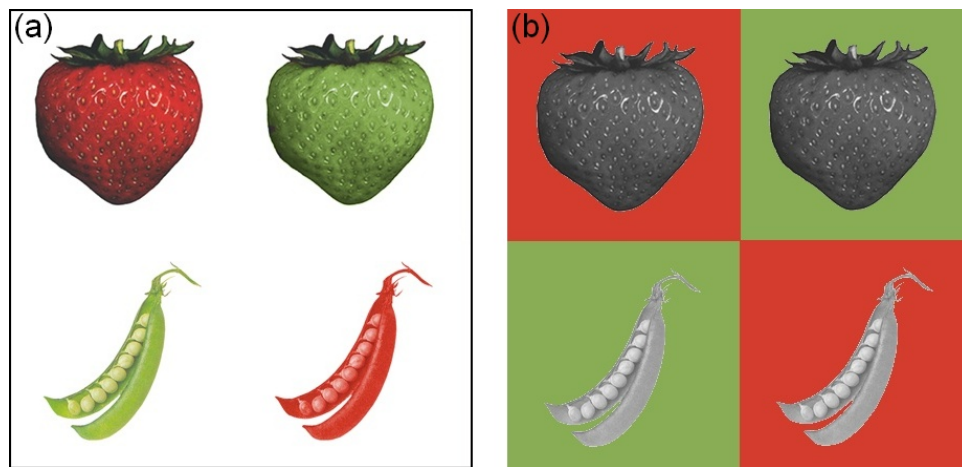


Figure 7: Examples of two objects in Experiments 1 and 2 are illustrated in their correct (left of figure sub-part) and incorrect (right of figure sub-part) colours. In (a) the colours are depicted on the surface of the objects. In (b) grey-scale versions of the objects are shown presented on coloured backgrounds.

Thirty-six coloured pictures of every-day objects served as stimuli (a full list can be found in Appendix 2). All items were ‘colour-diagnostic’ (i.e. the objects were associated with a typical colour). The stimuli were rendered in two of six basic colours (red, green, orange, yellow, blue/purple, brown), once in their typical (correct) and once in an atypical colour

(incorrect). Each stimulus was then again converted to gray-scale and the colour that had previously depicted the surface of the item filled the object's surround. Each of the six colours appeared equally often as both a correct and an incorrect colour. Stimulus colour was modified using the GIMP 2.6 image manipulation software. All items were rendered on 222 x 222 canvases. Example stimuli are displayed in Figure 7.

Eight participants, none of whom took part in the experiment, completed colour typicality and familiarity ratings verifying that the items selected were well-known and were correctly assigned to correct and incorrect colour conditions.

Design and Procedure

A 2 (colour location, item surface / background) x 2 (colour, correct / incorrect) within-participants design was used with each participant viewing each of the thirty-six items four times. Therefore participants completed one hundred and forty-four trials, which were arranged in a random order and viewed in two blocks. On each trial a single stimulus was presented for an unlimited duration in the centre of the screen. On a majority of trials (for all colours bar red), participants were required to report the name of the object as quickly and as accurately as possible. On a minority of trials (22%) however, the colour red was present in the array (either on the object's surface or in the background) and, in this case, participants were required to report the colour (i.e. "red") and not the object's name. Accuracy was hand-scored by the experimenter and the response latency was measured from the onset of the stimulus using a voice trigger. Each trial sequence was initiated with a 350ms central fixation cross followed by the stimulus, which was displayed until a response was made. An interval of 1250ms preceded the onset of the next trial. Participants were familiarised with this routine in a practice session where it was emphasised that dysfluent responses (stuttering, repairs etc.) and non-speech sounds (e.g. lip smacking,

coughing etc.) should be avoided. Immediately prior to the experimental session participants studied a booklet that displayed each item in gray-scale along with its most frequently used label in order to minimise variability in naming.

Results

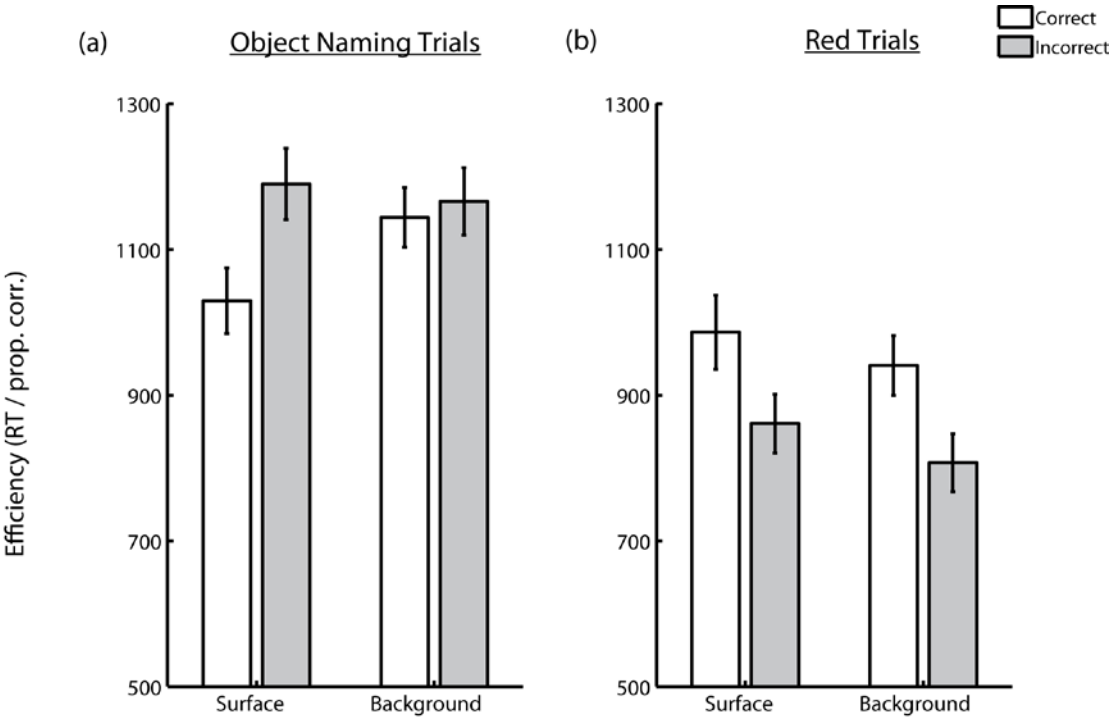


Figure 8: Response efficiency (RT / prop. corr.) and the standard error of this mean is displayed for naming (a) and red (b) trial types for correct (white bars) and incorrect (grey bars) colour conditions. Mean efficiency scores are separated along the x-axis according to whether the colour was depicted the item’s surface or the background.

For each participant an outlier analysis was used to remove speech production latencies that exceeded 2.0 standard deviations above or below the mean (4.14 %) and incorrect response trials (14.3 %). The RT and accuracy data are displayed in Table 3 (‘naming’ trial types) and Table 4 (‘red’ trial types). There was no evidence of a speed-accuracy trade-off. To facilitate the presentation of the results (here and in Experiments 2, 3 and 4 too), performance efficiency was computed (speech production latency (ms) / proportion

correct, Townsend & Ashby, 1983) and is displayed for ‘naming’ (a) and ‘red’ (b) trial types in Figure 8.

Naming Trials

Response efficiency was analysed using a repeated measures ANOVA with colour-type (correct / incorrect) and colour-location (item surface / background) as factors. These factors significantly interacted ($F(1, 23) = 13.975$, $p = 0.001$), which reflected a reliable benefit from colour-shape consistency when the colour fell on the surface of the object ($t(23) = -7.603$, $p < 0.001$), but not when it appeared in the background ($t(23) = -0.883$, $p = 0.386$).

Table 3: Speech production latencies and the proportion of correct responses for ‘naming’ trials. The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item’s surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	878.63	963.37	0.87	0.85
Incorrect Colour	963.72	978.87	0.83	0.85

Red Trials

Response efficiency on red trial types was analysed using a repeated measure ANOVA again including colour-type (correct / incorrect) and colour-location (item surface / background) as factors. Only a significant main effect of colour-type occurred ($F(1, 23) = 9.482$, $p = 0.005$), with significantly more efficient performance when object identity was incompatible with the colour response compared to when it was compatible. Unlike the pattern of performance seen for naming, the effect of the object name did not interact with the location of the colour ($F < 1$).

In all conditions, the majority of erroneous responses made on ‘red’ trials were due to inappropriate naming of the object (with the correct label) rather than the correct colour (percentage of errors in each condition where object name was produced: Surface Correct: 94%, Surface Incorrect: 93%, Background Correct: 80%, Background Incorrect 85%). The speech onset latencies on error trials were analysed when objects were presented in their appropriate colour. There were too few errors to allow the analysis to take place on trials where the objects were presented in incorrect colours. There were no differences in the speech onset latency of erroneous responses according to whether the item’s surface or surround was depicted in the colour ($t(12) = 0.172$, $p = 0.866$, for the 13 participants who contributed data).

Table 4: Speech production latencies and proportion correct responses for ‘red’ trials. The results are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item’s surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	799.33	770.08	0.83	0.84
Incorrect Colour	766.24	709.63	0.91	0.9

Discussion

These findings are consistent with the previous literature demonstrating that object naming is more efficient when items appears in their correct relative to their incorrect colour (Joseph, 1997; Joseph & Proffitt, 1996; Nagai & Yokosawa, 2003; Naor-Raz, et al., 2003; Nicholson & Humphrey, 2001; Price & Humphreys, 1989; Tanaka & Presnell, 1999). The new result is that, when objects were presented along with the correct colour, it was difficult for participants to ignore the name and name the colour, at least under the present conditions where object naming was the most likely response. This interference effect is

consistent with the irrelevant object identity being activated, but particularly if it carries a familiar relationship with the colour. This was confirmed by the error analysis, where the great majority of errors on colour naming trials reflected naming of object identity rather than the colour.

Interestingly, though the positive effect of colour on object naming depended on the colour falling on the object's surface and not in the background, the interference effect from the object name did not. One reason for this might be that, on object naming trials, there was insufficient time for the background colour to be processed before the object name was retrieved. Effects might then be confined to when the colours are centrally presented, when they fall on the surface of the objects. A pure temporal account of the results does not fit easily with the data however, since object naming was slower than colour naming (Figure 8), yet effects of the background colour were found on colour naming. A contrasting possibility is that object naming is only affected when the colour and shape access a common 'bound' perceptual representation, sensitive to both the shape and the surface colour of the object. If there is more rapid access to this perceptual representation when objects carry the familiar colour on their surface, then object naming will benefit relative to when the surface colour is incorrect or to when the colours are in the background. On the other hand, interference from the object on colour naming might arise from competition at the stage of name retrieval, and this competition might be driven by increased activation of semantic as well as perceptual representations, when colour information is correct. Semantic representations may be directly activated when the correct colour information is present in the display (on the background as well as the surface of the object). The idea that colour might access semantic representations independent of stored perceptual knowledge was proposed by Ostergaard and Davidoff (Ostergaard & Davidoff, 1985). The proposal is also supported by neuropsychological data. For example, Soto and Humphreys (2010)

reported evidence from a patient with Balint's syndrome who was prone to make illusory conjunctions to visual displays. Soto and Humphreys reported that there was illusory report of a colour if it was presented with a word that was semantically associated with another colour (e.g., reporting green to a red patch when the word grass appeared simultaneously). Thus colour report may be mediated by direct activation of semantic knowledge, and be influenced by an object name even when the object name and colour are physically separated. In addition to semantically-based competition for colour name retrieval, though, there may also be effects based on stronger activation of the object's perceptual representation when the surface colour is correct. This may have been masked under conditions where semantic competition arises. Experiment 2 sought to distinguish competition driven by perceptual and semantic representations by using briefer exposure durations, where effects of perceptually-driven competition might be more evident.

Experiment 2: Brief stimulus durations

Method

Participants

Twenty-four female undergraduate students at the University of Birmingham participated in exchange for course credits (18-23, 4 left-handed). They were recruited according to the same criterion as Experiment 1.

Stimulus, Design, Procedure

The method was identical to that outlined in Experiment 1 except that the previously unlimited stimulus duration was reduced to 100ms.

Results

Speech production latencies that exceeded 2.0 standard deviations above or below the mean (3.5%) or were incorrect response trials (22.2%) were removed. The RT and accuracy data are displayed in Table 5 ('naming' trial types) and Table 6 ('red' trial types). Performance efficiency was computed (speech production latency (ms) / proportion correct) and is displayed for 'naming' (a) and 'red' (b) trial types in Figure 9.

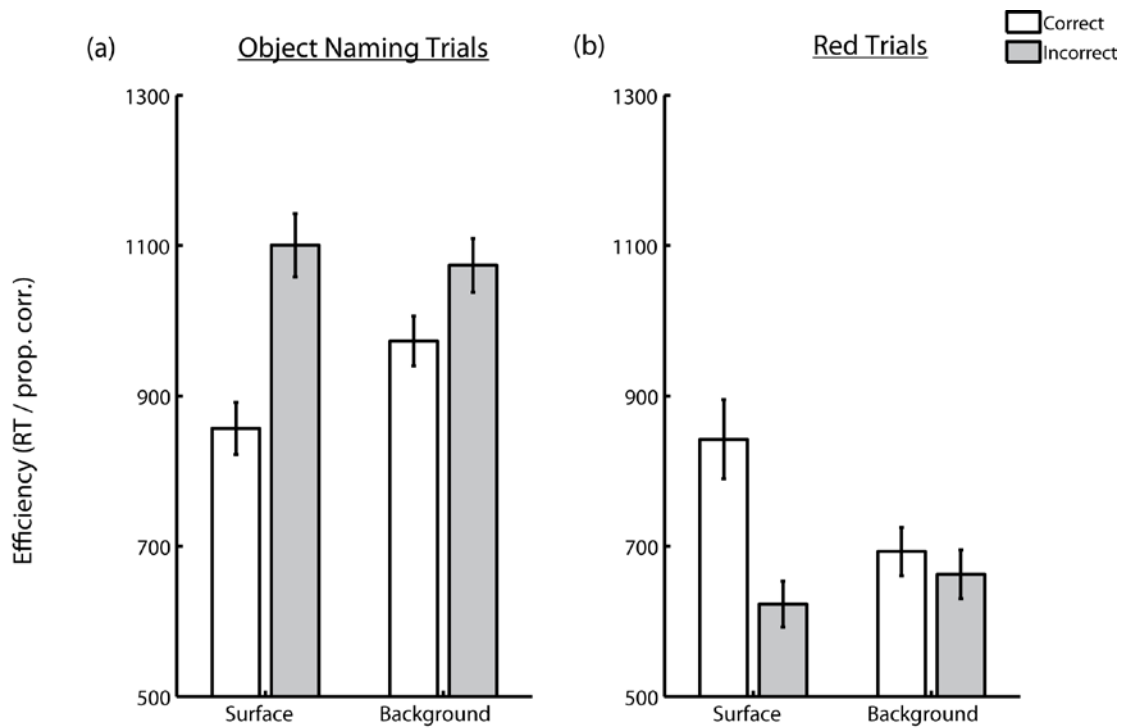


Figure 9: Response efficiency is displayed (RT / prop. corr.), and the standard error of this mean, for naming (a) and red (b) trial types for correct (white bars) and incorrect (grey bars) colour conditions. The x-axis separates performance according to whether the colour was depicted on the item's surface or its background.

Naming Trials

Response efficiency was analysed using a repeated measures ANOVA involving colour – type (correct / incorrect) and colour-location (item surface / background). Significant effects of both colour-type ($F(1, 23) = 100.006$, $p < 0.001$) and location ($F(1, 23) = 5.861$, $p = 0.024$) were returned. In addition these factors interacted ($F(1, 23) = 18.937$, $p < 0.001$). Whilst in both location conditions colour-shape consistency improved naming efficiency, the magnitude of this benefit was greatest when colours appeared on the surfaces of the objects (M difference: 243.825 ms) rather than in the background (M difference 100.85 ms).

Table 5: Speech production latency and proportion correct responses for ‘naming’ trials. The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item’s surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	691.76	751.41	0.82	0.78
Incorrect Colour	752.55	777.64	0.69	0.73

Red Trials

Response efficiency on red trials was analysed using a repeated measure ANOVA again including colour-type (correct / incorrect) and colour-location (item surface / background) as factors. A significant effect of colour was found ($F(1, 23) = 24.947, p < 0.001$), and this interacted with location ($F(1, 23) = 9.916, p = 0.004$). There was a significant benefit of colour-shape consistency when the colour appeared on the surface of items ($t(23) = 4.865, p < 0.001$) but not when it appeared in the background ($t(23) = 0.952, p = 0.351$).

As in Experiment 1, incorrect object naming accounted for a greater percentage of ‘red’ errors when the colour depicting an item’s surface was consistent with its shape (the percentage of errors where the object names produced were: Surface Correct: 89%, Surface Incorrect: 85%, Background Correct: 85%, Background Incorrect 70%). When speech onset latencies on incorrect response trials were analysed, participants erroneously reported the names of items faster when colour was depicted on the surface of the object rather than the background ($t(10) = -2.670, p = 0.023$, based on data from the 11 subjects who contributed data).

Table 6: Speech production latency and proportion correct responses for ‘red’ trials. The results are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item’s surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	626.10	581.99	0.77	0.86
Incorrect Colour	571.38	530.50	0.93	0.83

Discussion

As reported in Experiment 1, object naming was more efficient when items were shown in their consistent colour, and the effects are larger when the colour was bound to the surface of the object relative to when it was presented in the background (though some effects of having the correct colour in the background were apparent). Matching Experiment 1, I also found that objects interfered with colour naming (on ‘red’ trials) when there was an association between the colour and the object (harder to name red to strawberry than to banana, when both were depicted in red). Here however, this interference effect on colour naming was also modulated by the location of the colour in relation to the objects. Unlike Experiment 1, interference from the irrelevant shape was observed only when colour fell on the object’s surface. This result is consistent with interference arising from the familiar colour-shape representation gaining fast access to stored perceptual knowledge of the object, which then disrupts colour naming by generating greater competition for naming. The contrast to Experiment 1 suggests that the nature of the interference on colour naming can change according to the processing time available. Under brief presentation conditions, effects on access to stored perceptual representations are stronger than effects mediated by activation of semantic knowledge by the background colour. Under prolonged exposure conditions, however, effects can also emerge based on independent access of colour and

objects to semantic knowledge (from background as well as surface colours), as in Experiment 1.

The results on the efficiency of naming 'red' were supported by error data. Participants frequently made errors by naming the identity of the object rather than the colour, and these incorrect identity responses were faster when the objects were in the correct colour compared with the incorrect colour.

However, a counter argument can be made to our proposal that short exposures emphasise perceptual representations. This is there may have been data limitations on processing the background colours in Experiment 2, since the colours fell in more peripheral locations than the surface colours. Under limited exposure conditions, participants might have had to shift attention to the more peripheral location to name the colours, and then might have processed the object less. The net result might be a weaker effect of the object on naming the background colour relative to the surface colour. One piece of evidence against this is that, on object naming, background colour had some effect in Experiment 2 (short exposures) whilst it had no reliable effect in Experiment 1 (long exposures). Data limitations seemed not to be critical for the effects of colour on object naming. Nevertheless, this counter argument was tested in Experiment 3, where I shifted fixation to the background, to ensure that background colours could be processed without shifts of attention.

Across-Experiment Analysis

For completeness, overall comparisons across Experiment 1 and 2 were made.

Naming Trials

Response efficiency was analysed using a repeated measures ANOVA involving colour – type (correct / incorrect) and colour-location (item surface / background) as within-subject factors and experiment duration (unlimited / brief) as between. Significant effects of duration ($F(1, 46) = 5.879, p = 0.019$), colour-type ($F(1, 46) = 141.88, p < 0.001$) and location ($F(1, 46) = 32.326, p < 0.001$) were returned. In addition colour-type and location interacted ($F(1, 46) = 18.937, p < 0.001$). Whilst in both location conditions colour-shape consistency improved naming efficiency, the magnitude of this benefit was greatest when colours appeared on the surfaces of the objects (M difference: 202 ms) rather than in the background (M difference 62 ms). Colour-type also significantly interacted with experiment duration ($F(1, 46) = 13.519, p = 0.001$). In both Experiment 1 and 2 object naming was more efficient when items were congruently coloured, however this benefit was greatest when stimuli were presented briefly (Mean difference: 172.337 ms vs. 91.038ms). This is consistent with the suggestion that colour may be of particular benefit in conditions of degradation; here this is created by brief display duration.

Red Trials

Again, response efficiency was analysed using a repeated measures ANOVA involving colour –type (correct / incorrect) and colour-location (item surface / background) as within-subject factors and experiment duration (unlimited / brief) as between. Significant effects of duration ($F(1, 46) = 67.906, p < 0.001$), colour-type ($F(1, 46) = 23.493, p < 0.001$) and location ($F(1, 46) = 6.936, p = 0.011$) were returned. Duration interacted with location ($F(1, 46) = 18.272, p < 0.001$); when participants were not time-limited

(Experiment 1) 'red' responses were more efficient when the colour was depicted on the items surface (923.583 ms) than the surround (1154.737). By contrast, participants 'red' responses to briefly presented stimuli were not clearly affected by the colour location (i.e. the confidence intervals overlap). There was also a borderline interaction between duration and colour-type ($F(1, 46) = 4.031, p = 0.051$). In both Experiment 1 and 2 when 'red' was congruent with the object, performance was not as efficient. This interference effect was greater when items were presented briefly (Mean Difference: 124.726) than for an unlimited duration (Mean difference: 51.661). Lastly, the interaction between colour-type and location was significant ($F(1, 46) = 19.217, p < 0.001$) indicating that for both experiments colour-congruency interfered with naming 'red' when the hue depicted the objects surface but not the surround.

Experiment 3: Brief presentations with fixated backgrounds

Method

Participants: Twenty-four undergraduate and postgraduate students at the University of Birmingham were recruited according to the same criterion as Experiment 1 and participated in exchange for course credits (18-25, 5 male, 3 left-handed).

Stimulus, Design, Procedure

The method was identical to that outlined in Experiment 2 except that instead of the stimuli always appearing in the centre of the screen their position was offset to the left/right by 111 pixels. The outer left/right of the stimulus was therefore central to the display (Figure 10).

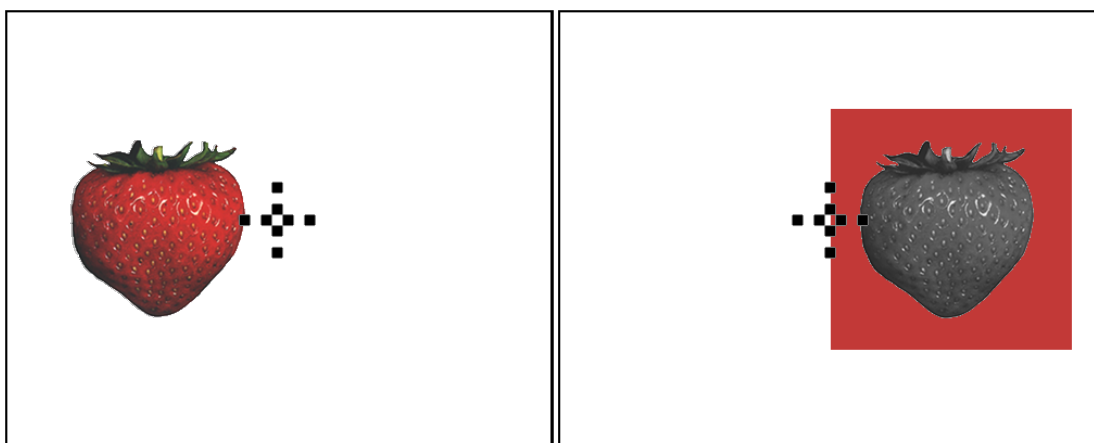


Figure 10: Example 'red' surface and background stimulus displays in Experiment 3. The central cross was offset on stimulus onset, but is depicted here as a dashed line to illustrate the location of fixation.

Results

An outlier analysis removed speech production latencies that exceeded 2.0 standard deviations above or below the mean (3.2 %) and incorrect response trials (24%). The data RT and accuracy data are displayed in Table 7 ('naming' trial types) and Table 8 ('red' trial types). Performance efficiency was computed (speech production latency (ms) / proportion correct) and is displayed for 'naming' (a) and 'red' (b) trial types in Figure 11.

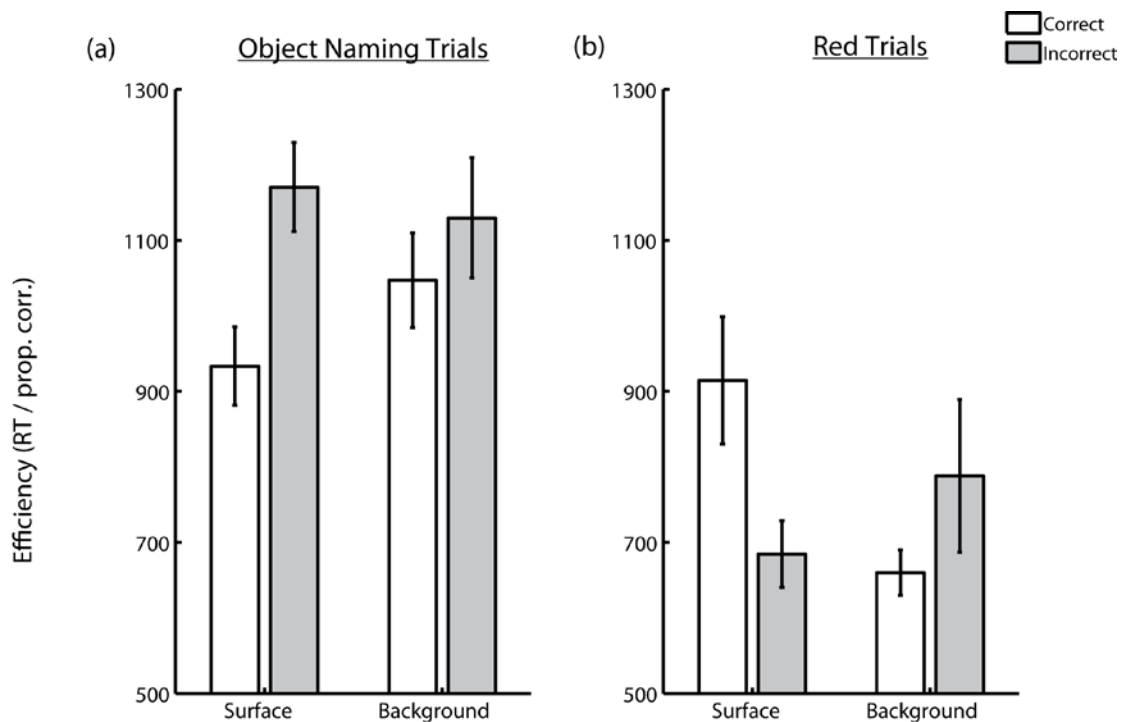


Figure 11: Response efficiency is displayed (RT / prop. corr.), and the standard error of this mean, for naming (a) and red (b) trial types for correct (white bars) and incorrect (grey bars) colour conditions. The x-axis separates performance according to whether the colour was depicted on the item's surface or its background.

Naming Trials

Response efficiency was analysed using a repeated measures ANOVA involving colour-type (correct / incorrect) and colour-location (item surface / background). The effect of colour-type was significant ($F(1, 23) = 25.606, p < 0.001$) and this factor interacted with colour-location ($F(1, 23) = 17.362, p < 0.001$). Consistent colour-shape information

significantly facilitated naming efficiency when it was depicted on the object's surface ($t(23) = -8.469, p < 0.001$) but not when it fell in the background ($t(23) = -1.895, p = 0.071$).

Table 7: Speech production latency and proportion correct responses for 'naming' trials. The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item's surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	701.98	778.29	0.78	0.77
Incorrect Colour	792.64	767.91	0.69	0.72

Red Trials

Response efficiency on red trials was analysed using a repeated measure ANOVA again including colour-type (correct / incorrect) and colour-location (item surface / background) as factors. These factors reliably interacted ($F(1, 23) = 8.026, p = 0.009$). There was interference of based on colour-shape consistency when the colour appeared on the surface of an item ($t(23) = 2.550, p = 0.18$) but not when it appeared in the background ($t(23) = -1.474, p = 0.154$).

The majority of errors on 'red' trials reflected (inappropriate) production of the object's name, accounting for the greatest percentage of errors when the colour depicted on the item's surface was consistent with its shape (the percentage of errors Surface Correct: 94% vs. Surface Incorrect: 56%, Background Correct: 88%, Background Incorrect 76%). Error naming times (for the production of the inappropriate object name) were faster when the correct colour fell on the object's surface (M: 652.23 ms) rather than the surround (M: 885.06 ms) ($t(15) = -2.570, p = 0.02$; results for the 16 participants who contributed data).

Table 8: Speech production latency and proportion correct for ‘red’ trials. The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item’s surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	634.27	563.25	0.75	0.87
Incorrect Colour	602.49	554.24	0.91	0.80

Discussion

The findings replicated those reported in Experiment 2, even though the colours fell at fixation in the background condition. Here participants should not have had to shift attention to perceive the background colour, but still no effect of the congruency of the object and the background colour was apparent on colour naming. The results emphasise that the limited exposure durations highlight access to perceptual representations, even when the colour processing is not subject to data limitations when colours fall in the background relative to when they appear on the surface of objects.

Experiment 4: Colour Naming

In Experiment 4 I ran a pure colour-naming task. This control experiment sought to address the possibility that reported effects were due to chromatic differences rather than colour-shape associations.

Method

Participants: Eight students at the University of Birmingham were recruited according to the same criterion as Experiment 1 and participated in exchange for course credits.

Stimulus, Design, Procedure

The method was identical to that outlined in Experiment 2 except that participants engaged in a colour-naming task only i.e. participants were required to name the colour of all items not just the red ones.

Table 9: Speech production latency and proportion correct for naming colours (excluding 'red'). The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item's surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	742.03	728.02	0.98	1
Incorrect Colour	841.48	712.38	0.94	0.99

Results

An outlier analysis removed speech production latencies that exceeded 2.0 standard deviations above or below the mean (5.96%) and incorrect response trials (1.6 %). The data RT and accuracy data are displayed in Table 9 and Table 10. Performance efficiency was computed (speech production latency (ms) / proportion correct).

Table 10: Speech production latency and proportion correct for colour naming red trials. The data are displayed for correctly and incorrectly coloured stimuli according to whether the hue was depicted on the item's surface or background.

	RT (ms)		Prop. Corr.	
	<i>Surface</i>	<i>Background</i>	<i>Surface</i>	<i>Background</i>
Correct Colour	674	623.2	0.98	1
Incorrect Colour	727.85	679.68	0.98	1

Response efficiency was analysed using a three-way repeated measures ANOVA involving colour-type (correct / incorrect), colour (red / not red) and colour-location (item surface / background). The effect of colour was significant ($F(1, 6) = 19.720, p = 0.004$). Naming the colour red was more efficient than all other chromatic labels ($M: 685$ vs. 779). There was no significant effect of either colour type ($F < 2$) or location ($F < 5$). Furthermore, there was no significant interactions between any of the experimental factors (all F 's < 2).

Discussion

In Experiment 4 colours were easier to name when they were correct for the object and when they fell on the surface of the object (but much less so when they fell in the background). Moreover, this occurred for red objects as well as for objects in other colours. In addition the colour red was more easily labelled than the other five colours. The overall advantage for red may be due to many factors – for example, that it is a short, high

frequency word, that red has strong attention-related associations (stop!) and so forth. More important is the fact that this did not interact with the effects of correct colouring or with the positioning of the colour on the surface vs. background of the objects.

The advantage for naming colours when objects are coloured correctly is consistent with fast access to integrated shape-colour representations, which enables colour to be quickly retrieved. The result contrasts with our earlier findings, which occurred under conditions in which object naming (rather than colour naming) was prioritised. When naming is prioritised I propose that object names, accessed more rapidly from correctly coloured stimuli, block colour naming. Importantly, there was no evidence here that it was harder to access the name 'red' when the objects were coloured correctly, perhaps due to subtle chromatic changes across the stimuli.

General Discussion

From four experiments I have shown strong effects of colour-object relations both on both object and colour naming. Moreover, I provide the first demonstration that the effects of object congruency on colour naming can be negative, so that colour naming is slowed and object naming responses sometimes made erroneously when the colour is correct for the object.

It has previously been demonstrated that object naming is more efficient when items are depicted in their correct rather than incorrect colour (Joseph, 1997; Joseph & Proffitt, 1996; Nagai & Yokosawa, 2003; Naor-Raz, et al., 2003; Nicholson & Humphrey, 2001; Price & Humphreys, 1989) and that these effects are not observed when the colour does not depict the items surface but falls in the background (Price & Humphreys, 1989). Here I confirmed these findings using photographs of diagnostic items and add to growing consensus that object-colour knowledge may play an important role in object recognition. I attribute the result to perceptual representations of objects being sensitive to the binding of the colour and shape, when colour occupies an object's surface. The stronger activation of the object's perceptual representation enhances name retrieval.

I also presented a novel version of an object-Stroop task. In the context of object naming being the majority response, I found that responses to occasional colours were disrupted when the colour was congruent with the object. Two aspects of this interference effect have been demonstrated. With prolonged stimulus exposures there was interference from the familiar pairing of object and colour when the colour fell in the background as well as when it appeared on the objects surface (Experiment 1). Here I attribute this to the colour and the object activating semantic knowledge independently. The semantic representation

of the object in turn activates the object's name, so that the name competes with that of the colour. There is an effect of familiar object-colour pairing because there is greater semantic activation when the familiar colour is presented along with the object (see Soto & Humphreys, 2010). I assume that this is a slow-acting process that takes place under prolonged presentation conditions.

The results on colour naming changed when the presentation durations were reduced. In this case there were effects of interference only when the colour fell on the object's surface, irrespective of whether fixation fell on the object's surface (Experiment 2) or the background (Experiment 3). Here I suggest that the effects reflect strong name competition driven by enhanced activation of the stored perceptual representation of the stimulus, which is sensitive to whether the object is depicted with its familiar colour surface. Colour naming is disrupted by the object's name, and, indeed, on a significant proportion of trials participants name the object instead of the colour.

Taking the effects on object and colour naming together, the present data provide strong evidence that our perceptual knowledge integrates shape and surface colour, rather than object recognition being solely based on object form (as proposed by 'edge-based' account of object recognition; Biederman & Ju, 1987). Depending on whether the stronger activation of the object naming is beneficial or detrimental to the task (for object and colour naming respectively), there are benefits or costs from depicting objects with their correct surface colours.

There are two final caveats however. First I note that I only presented objects that have diagnostic colours, and the present results may be confined to such stimuli for either of two reasons. One is that these items have more consistent shape-colour associations than other

stimuli and, as a consequence, our perceptual knowledge of these stimuli is more likely to incorporate colour as well as shape information. The second is that many items that have diagnostic colours also have relatively similar perceptual structures, as is the case for the fruits and vegetables used here. Colour may help differentiate between the perceptual structures of these items (see Price & Humphreys, 1989). As a result, the object will be named faster when in their standard colours and the object names will compete more strongly with the colour name, when colour naming is required. The second caveat is that the present results were obtained under conditions in which object naming was required on the majority of trials. Under these conditions, the task set was to name the object, and this may have led to the object name being accessed sufficiently rapidly to compete with the colour name. I note that, in experiments where the sole task is colour naming, presenting objects in their correct colours can facilitate performance (Ménard-Buteau & Cavanagh, 1984; Naor-Raz, et al., 2003), though it can then be unclear whether participants deliberately access an object's name in order to retrieve the colour name by association. In the present conditions I assume that the object name was not produced to aid colour naming, since the main finding is an interference effect, but the pervasive effect of object naming I observe may reflect the weighting for object naming in the main task. The boundary conditions that determine the present effect, and how much control participants can bring to bear on the interference from the object on colour naming, are important topics for future research.

CHAPTER 5

EVIDENCE FOR SPATIALLY PARALLEL BINDING OF LEARNED CONJUNCTIVE RELATIONS

Synopsis

Physiological evidence indicates that different visual features are computed quasi-independently (Hubel & Livingstone, 1987; Treisman, 1998). The subsequent step of binding features, to generate coherent perception, is typically considered a major rate limiting process, confined to one location at a time and taking 25ms or per item or longer (Treisman & Gormican, 1988). I examined whether these processing limitations remain once bindings are learned for familiar objects. Participants searched for objects which could appear either in familiar or unfamiliar colours. Objects in familiar colours were detected efficiently at rates consistent with simultaneous binding across multiple stimuli. Processing limitations were evident for objects in unfamiliar colours. The advantage for the learned colour for known targets was eliminated when participants searched for geometric shapes carrying the object colours and when the colours fell in local background areas around the shapes. The effect occurred irrespective of whether the non-targets had familiar colours, but was largest when non-targets had incorrect colours. The efficient search for targets in familiar colours held even when search was biased to favour objects in unfamiliar colours. The data indicate that learned bindings can be computed with minimal attentional limitations, consistent with the direct activation of learned conjunctive representations in vision.

Introduction

A major tenet of influential theories of human vision is that feature binding represents a critical limiting step, operating at only a single attended location at a time (Treisman, 1998; Treisman & Gelade, 1980). Typical evidence supporting this view is that search for targets comprising a conjunction of different features is slow (often taking around 25ms/item or longer) and linearly related to the number of non-targets present. Inefficient search for conjunction targets occurs even when search for each feature making up the conjunction is efficient and minimally affected by non-targets (search rates ~10ms/item or less) (Treisman & Gelade, 1980). It has been argued that search rates of under 10ms/item are inconsistent with a biologically plausible serial search process, with search slopes above 20ms/item reflecting the operation of serial selection processes (Treisman & Gormican, 1988). Such results suggest that, to code the conjunction of features that distinguishes targets from non-targets, attention must be serially applied to each stimulus in turn (Treisman, 1998; Treisman & Gelade, 1980).

Search for targets defined by a conjunction of features is not always inefficient, however. For example, when targets are distinguished by particular feature combinations (such as motion and form, Driver & McLeod, 1992; McLeod, Driver & Crisp, 1988; or stereoscopic depth and motion, Nakayama & Silverman, 1986) or when the features are highly distinct along the feature dimensions defining the target (Wolfe, Cave & Franzel, 1989), then conjunction search is efficient. In these circumstances, though, participants may be able to facilitate search by selectively inhibiting non-targets with one common feature that is distinct from the target (Dent et al., 2012; Treisman & Sato, 1990). Search can then be based on the uninhibited feature property that does distinguish targets and non-targets, without requiring that target features are bound. Outside of such special circumstances,

when the features comprising targets and non-target do not support selective non-target inhibition, can the attentional limits of binding conjunction features be reduced?

One potentially important factor is learning. Nearly all studies that have examined search for conjunction targets have used stimuli that have arbitrary relations between their features, such as colour and geometric shape, which have no a priori association. In contrast, numerous objects in our environment have specific rather than arbitrary feature relations – for example, living things have set, associated colours and do not take on arbitrary feature values in the real world. Currently we do not know how search proceeds for stimuli that have learned relations between their features and the theoretical tenet, that there are attentional limits on feature binding, is based on stimuli that are not characteristic of our environment. It is possible though that a sensitivity to familiar conjunctive relations, between shapes and colours say, may enable the brain to overcome some of the processing limitations apparent when we encounter stimuli with arbitrary feature relations. For example, familiar conjunctions of features may be stored together, by-passing the need to recruit attention to enable binding to take place (Rust & DiCarlo, 2010; Seymour, Clifford, Logothetis, & Bartels, 2009, 2010). Alternatively, learned connections between representations of co-occurring features may enable those representations to rapidly synchronize their firing (Singer & Gray, 1995), enabling familiar conjunctive targets to be selected efficiently.

Evidence that the binding of learned associations operates rapidly would be consistent with some form of ‘hard-wired’ coding. Using a dual-task procedure, Li et al. (2002) found that a central attentionally demanding letter discrimination did not compromise the ability of participants to detect a briefly presented peripheral animal or vehicle. Analogous results have been found using face stimuli requiring either gender discrimination (Reddy et al.,

2004) or face recognition (Reddy et al., 2006). This suggests that coding the relations between the features making up these stimuli, to enable identification to proceed, can take place without deploying attention. Van Rullen (2009) proposed that this was achieved by ‘hardwired binding’, which integrates features of familiar natural scenes and objects automatically and without serial attention. He proposed that this mechanism co-exists with an ‘on-demand’ system dealing with arbitrary and unfamiliar conjunctions by engaging visual attention. Against this, Evans and Treisman (2005) argued that apparent high-level identification of objects in scenes was in fact based on detecting particular features and that attention was required when identification depended on feature binding. Studies showing efficient detection of familiar stimuli lack control conditions demonstrating that performance is not efficient when the same features are present but not combined in a familiar manner. I take steps to include such control conditions here.

There is neurophysiological evidence too indicating that the same neural regions may not be required for binding once stimuli have learned feature relationships, and that learned feature relations are computed rapidly. For example, Walsh, Ashbridge and Cowey (1998) reported that trans-cranial magnetic stimulation applied to posterior parietal cortex selectively disrupted conjunction search when participants searched for novel shape-colour targets, but not once the colour-shape relations were learned. Given the role of posterior parietal cortex in guiding visual attention (Corbetta & Shulman, 2002), this result suggests that learned conjunctions may be selected using brain regions outside the circuit associated with attentional control. Furthermore, Lu et al. (2010) collected human electrophysiological recordings whilst participants viewed stimuli that have a ‘diagnostic colour’ (i.e. objects whose shape and colour are consistently associated). They found that ERP components indexing early perceptual processing (N1, N2 and P2) differentiated between correctly coloured stimuli and incorrect and gray-scale versions of the same items,

consistent with the involvement of early brain regions in computing learned conjunctive relations.

Matching these results are behavioral data from visual search too demonstrating efficient search once conjunctions of features are learned. For example there are asymmetrical search efficiencies for shape-conjunction targets in their correct orientation relative to when they are in a reflected, unfamiliar orientation ($Z_{vs. \Sigma}$), even though the same features distinguish the familiar from the unfamiliar shapes in each case (Wang, Cavanagh & Green, 1994). However, it can be argued that there is a qualitative distinction between binding within a feature domain (e.g., different form elements) and binding across domains (colour and form; see Humphreys, Hodsoll & Riddoch, 2009), and that attention is required particularly for cross-domain binding. For example, damage to posterior parietal cortex can be highly disruptive for colour-form binding but not for binding of form features (Humphreys et al., 2000, 2009).

In the present paper I set out to test whether targets defined by complex conjunctions of features, drawn from different processing domains (colour and form), could be detected efficiently if the feature relations were learned and not arbitrary. I report three main experiments. In the first experiment (Experiment 1a), I had participants search for a common object (the target: corn) presented amongst a set of other common objects (the non-targets: carrot, aubergine, lemon). The target and colour could be in their familiar (correct) colours (yellow corn, orange carrot, purple aubergine, yellow lemon) or they could be re-paired to carry unfamiliar (incorrect) colours (e.g., purple corn, yellow carrot, orange aubergine, purple lemon), with the target's colour always paired to the same non-target (lemon) (see Figure 12). In all conditions, targets were distinguished from non-targets by a conjunction of features (the conjunction of features making up its shape, plus

also its colour), and the difficulty of discriminating targets from non-targets on the basis of their feature relations was confirmed in baseline conditions when the stimuli were defined by arbitrary feature relations (where search was always relative slow with RT-display size functions of over 20ms/item). These baseline conditions provide evidence that there are limitations on binding when the same features do not form familiar conjunctions. I assessed whether there was a difference in search efficiency when the features enjoyed learned colour-shape relations (the correct colour displays) compared with the baseline conditions when the conjunctions were not learned (the incorrect colour displays). In Experiment 1a I report that search for a familiar colour-form conjunction was uniquely efficient, compared with the baselines. In Experiment 1b I assigned the same colours to geometric forms and showed that the effects were not caused by the target colour per se – shapes carrying the correct colour from Experiment 1a were not searched for more efficiently than those carrying the incorrect colour. In Experiment 1a I attempted to maximise the contrast between learned and arbitrary conjunctions by having the non-targets always carry the same colour relation as the target – that is, non-targets were correctly coloured when the target was correctly coloured, and they were incorrectly coloured when the target was incorrectly coloured. However, to ensure that differences in search were due to the learned target colour (yellow), and not to participants using the familiar non-target colours to guide search to the target, I conducted further control experiments. In Experiment 1c I presented the same common objects as in Experiment 1a, but this time the colours were assigned to background regions around each shape. In this case, participants could use the colours on the background regions around non-targets to guide search to targets when all the items were assigned their correct colours, and they were explicitly advised to adopt this strategy if they could. Despite this, there was no benefit for targets on correct colour backgrounds. In Experiment 2a I generalised the results from Experiment 1 to different stimuli (target = a pepper) and evaluated further the

effect of the non-target colour by orthogonally varying whether targets and non-targets were in correct or incorrect colours. In all cases there was efficient search for correctly coloured targets, with performance being best for correctly coloured targets when the non-targets were incorrectly coloured. A further control study, Experiment 2b, showed that there was no advantage in search for geometric shapes carrying either the correct or the incorrect colours of the objects in Experiment 2a. In Experiment 3 I evaluated whether the advantage for familiar colour-form conjunction was due to a top-down set adopted when we search for a known object. For example, when asked to search for ‘corn’ we might strategically adopt the set of looking for yellow, given the association between the colour and shape of this stimulus. To test this I biased search against the familiar conjunction by making targets in incorrect colours more likely than targets in correct colours. I show that the likelihood manipulation was successful since, on target absent trials, eye movements were biased to non-targets carrying the incorrect target colour. Despite this there remained an advantage for targets in their correct colour, which were still detected efficiently. Taken together the data suggest that target shapes carrying their correct, learned colours escape the attentional limitations that affect arbitrary conjunctions of the same features in visual search. This runs counter to the idea that colour-form binding necessarily requires attention, since this predicts that the same attentional limitations should arise in all cases, since attention is required to bind the features before accessing knowledge of the feature bindings. I discuss the implications for theories of attention and object perception.

Experiment 1a: Three object colours, equally likely

Method

Participants

Ten students and employees at the University of Birmingham took part in the experiment (3 male, 8 right-handed, mean age 33). All participants had normal or corrected vision and gave informed consent.



Figure 12: The stimulus pairings used in Experiment 1.

Stimuli

There were four pictures depicting corn, lemon, aubergine and carrot. Each item was selected because it has a diagnostic colour; this is that the shape and colour were highly associated. Each item was rendered in three different colours: yellow (diagnostic for corn), orange (diagnostic for carrot) and purple (diagnostic for aubergine). Colours were exchanged using the colour picker tool provided in GIMP 2.6 image manipulation software. All stimuli were presented on white equiluminant background were scaled to 57 x 57 pixels subtending approximately 1.8° x 1.8°. Examples are illustrated in Figure 12.

Design and Procedure

Participants were required to search a display of items for a target corn stimulus. Arrays consisted of 4, 8, or 12 stimuli, one of which would be the target on 50% of the trials. Targets were presented equally often in yellow (target-correct colour), orange (target-incorrect colour) or purple (target-incorrect colour). Images of carrots, aubergines and lemons served as non-target stimuli and there was at least one present on each trial, with additional numbers sampled randomly from the three types of non-target in each colour condition. For every trial the appropriateness of the colour-shape association was consistent across target and non-target items (i.e., when the target was correctly coloured so were the non-targets; when it was incorrectly coloured, so were the non-targets). The colour of the target always matched the colour of the non-target lemon (see Figure 12).

The stimuli were randomly assigned to a location on an invisible circle. From these initial co-ordinates items were shuffled a further 10 pixels in any direction whilst ensuring they were a minimum distance of 200 pixels from central fixation. Location randomisation was constrained to ensure that the minimum distance between stimuli was 70 pixels and that stimulus density was roughly equal across the display to avoid local clustering. Stimulus presentation and response collection was controlled using E-Prime 2.0.

Participants viewed stimuli on a white display (33° x 26°) in a darkened room at a distance of approximately 65cm. They were required to judge whether a target was present or absent and to respond with a key-press as quickly and as accurately as possible. These instructions were given verbally and reiterated in written form at the start of the testing session. Experimental sessions were preceded with a practice session to familiarise participants with the task and ensure that they could correctly identify target items.

Participants completed 5 blocks of 360 trials (180 target present, 180 target absent), generating 100 trials for each target present condition at each display size.

Results and Discussion

Target present trials

In Figure 13 I present a combined measure of the speed and accuracy (RT/prop. correct) of responding to correct and incorrectly coloured targets in Experiment 1. Significance levels were Greenhouse-Geiser (GG) corrected where required. There was a reliable interaction between the factors target colour and the display size ($F(1.072, 9.650) = 6.28, p = 0.03$ GG) indicating more efficient search for correctly coloured targets across the display sizes. The search rate for correctly coloured targets was consistent with spatially parallel search (10ms/item) while that for incorrectly coloured targets was more than twice as slow (22 ms/item).

It is possible that the efficient search for correctly coloured targets stemmed from an expectation that the target could be its correct colour (yellow) after a correctly coloured object had been encountered. To test this I performed ‘carry-over’ analyses. Target present trials were separated according to whether the immediately preceding trial contained a target with the same colour, a target with a different colour or no target (target absent trial). Although reaction times were speeded when the immediately preceding stimulus had the same colour as the current target, the advantage for correct over incorrectly coloured targets held when the target was absent on the preceding trial ($F(2, 18) = 4.79, p = 0.049$, GG), when there was a target in a different colour ($F(2, 18) = 8.7, p = 0.015$, GG) and

when there were identical targets on consecutive trials ($F(2, 18) = 9.07, p = 0.002$) (Figure 14).

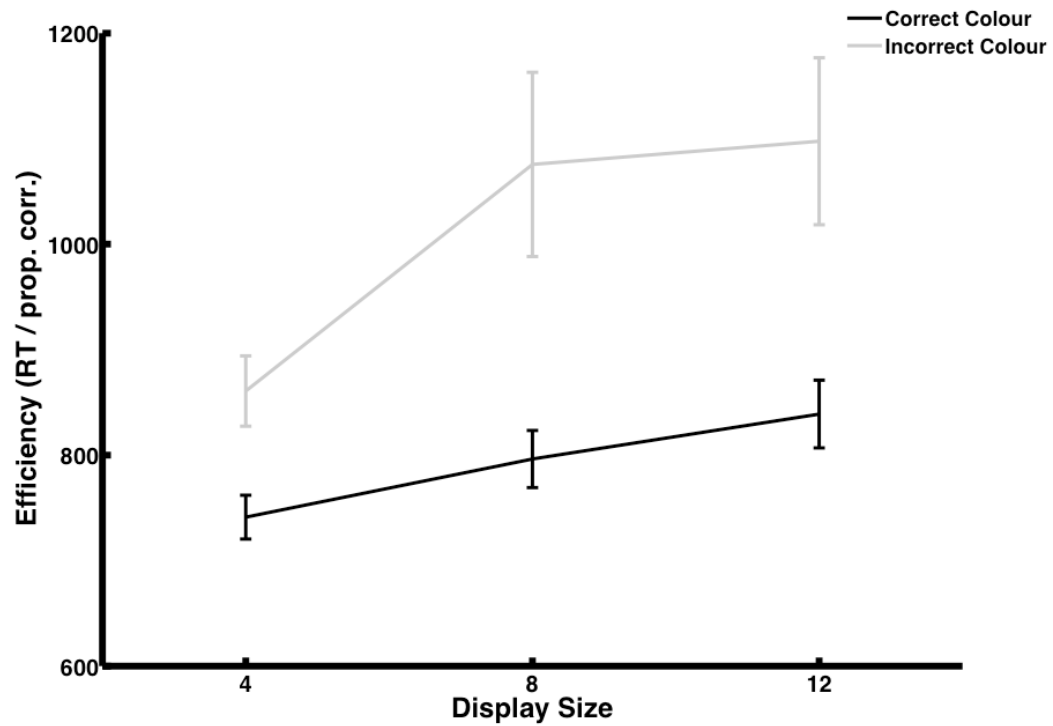


Figure 13: The mean efficiency (RT/prop. corr.) for search for targets in the correct and incorrect colours as a function of the different display sizes (4, 8 and 12) in Experiment 1a. Error bars = 1 SE.

There was relatively slow search for targets in incorrect colours (search rates > 20 ms/item), consistent with serial attention being required to distinguish targets and non-targets defined by arbitrary conjunctions of features. These attentional limitations were reduced when targets had the correct colour, when the search rate was within a range consistent with spatially parallel search (Treisman & Gormican, 1988).

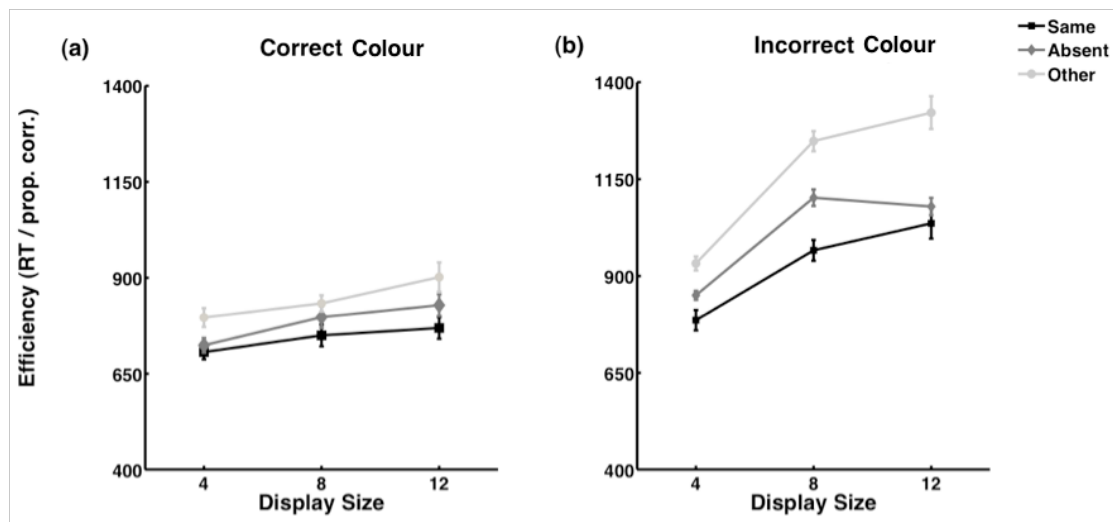


Figure 14: Experiment 1a: The mean efficiency (RT/prop. corr.) for search for correctly coloured (a) and incorrectly coloured targets (b) as a function of whether the preceding display had a target that was the same colour, a different colour or no target (absent).

Target absent trials

The efficiency of search on target absent trials is shown in Figure 15. There was a reliable main effect of colour type ($F(1, 9) = 38.413, p < 0.001$) and display size ($F(2, 18) = 116.461, p < 0.001$), and the interaction between these factors approached significance ($F(2, 18) = 4.086, p = 0.06, GG$). Target absent response efficiency decreased as a function of display size. At display sizes 4 and 8 performance was more efficient for correctly coloured relative to incorrectly coloured displays ($t(9) = -4.705, p = 0.001$) and 8 ($t(9) = -9.7, p < 0.001$).

These data on absent trials suggest that participants may be able to search faster through displays with correctly coloured objects than displays where the objects are coloured incorrectly, even when the items do not match any expectation for the target, at least when the display sizes are 8 or fewer. Search on absent trials was also slow and strongly affected by the display size (>60 ms/item). With such slow search, RTs may be faster if individual non-targets can be rejected more easily. There may be an advantage for correctly coloured objects here because these items may be identified more rapidly (e.g., see Ostergaard &

Davidoff, 1985; Price & Humphreys, 1989). However, if this was the case then we might expect the advantage for correctly coloured items to increase at the larger display sizes, when more non-targets have to be identified and rejected. An alternative is that correctly coloured (non-target) objects guide attention more efficiently even when they are not specified as part of the target memory set, at least when the display is not too cluttered (e.g., at display sizes 4 and 8). To produce efficient guidance at larger displays, the correctly coloured item might also have to match the ‘template’ for the target (cf. Duncan & Humphreys, 1989), as was the case for present trials here (Figure 13).

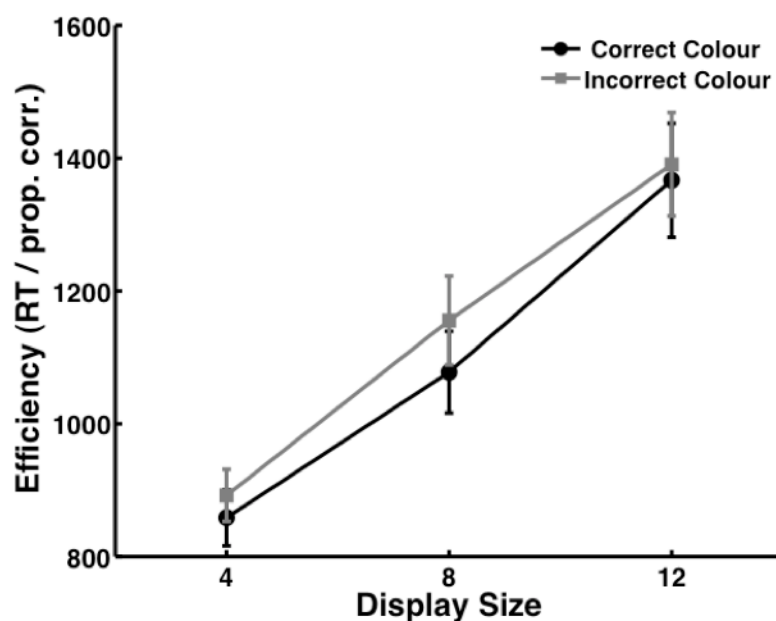


Figure 15: Target absent response efficiency is shown as a function of display size and is separated according to the appropriateness of the target colour.(Experiment 1a).

The slow search here on target absent trials does not detract from the efficient search for correct (learned) conjunction targets on target present trials. Note that the target could have one of three colours in the experiment, as could the non-targets, so that participants would have considerable uncertainty when searching the displays – especially when a target was

not available to guide the search process. Under such circumstances re-checking of items in the display can inflate search slopes.

Taking the data from present and absent trials together, the results indicate that there is efficient guidance of attention to correctly coloured targets which is not determined by the immediately temporal context of having just seen a target carrying its standard colour. However, various counter-arguments can be made. I discuss three. One is that the colours in Experiment 1a were differentially salient, with yellow being easier to select as a target than orange and purple. This could have led to more efficient search for yellow than purple or orange corn. This was tested in Experiment 1b, where I ran a control experiment where participants searched for a conjunction of colour and geometric form, with the colours extracted from the objects used in Experiment 1a. Would there be uniquely efficient search for the yellow-form conjunction?

A second possibility is that participants used the colours of the non-targets, rather than the colour of the target, to guide search. In Experiment 1a the colour assignment of the targets and non-targets co-varied. This meant that, as soon as participants detected that non-targets were in the correct colour, they might use this information to direct search to the correct target colour (to yellow corn). On the other hand, when the non-targets were in incorrect colours it might have been more difficult to guide search to a particular coloured target, since the non-target and target colours did not have a learned relationship. This possibility was explored in Experiment 1b where the same items were presented with the same contingencies between target and non-target colours, but with the colours in the local background of items rather than falling on the surfaces of the objects. Would detecting the correct colour-shape relation for a non-target then help guide search to the correct target colour? Experiment 2 tested the possibility further by orthogonally varying target and non-

target colour assignments, so that the target colour could not be predicted from the colours of non-targets.

The third alternative account can be couched in terms of Guided Search (Wolfe, 1994). The carry-over analyses (Figure 14) indicate that the advantage in search efficiency was not due to participants holding an expectation of the target in its correct colour, set from the immediately preceding trial. However, it could still be that the faster search for correctly coloured items reflected a bias for the correct colour, which was maintained across the whole experiment. That is, there may be top-down guidance for search for correctly coloured objects but not for incorrectly coloured objects, irrespective of trial-by-trial fluctuations, which arises due to the learned colour-shape association. Perhaps if told to look for ‘corn’, and the items are coloured, then participants retrieve their knowledge of the likely colour of the target in order to bias search. Consistent with this argument is evidence showing that visual search can be influenced by associative relations between non-targets in a display and a target that participants are set to detect (e.g., search for a motorbike is affected by the presence of a crash-helmet; Moores, Laiti & Chelazzi, 2003; Telling, Kumar, Meyer & Humphreys, 2010). To assess effects of predicting the target’s colour, I conducted Experiment 3 in which targets appeared in only 2 colours (yellow or purple corn, paired with the same colour as in the first experiment), and I biased the likelihood of each target appearing in favour of the incorrect over the correct colour (the purple target was twice as likely to occur as the yellow target). Is there still efficient search for familiar colour-form conjunctions when participants are set for targets in the incorrect rather than the correct colour?

Experiment 1b: Three target colours with geometric forms

I tested whether the efficiency of detecting correctly coloured corn targets was due to an intrinsic saliency of the hue yellow. To examine this Experiment 1a was replicated substituting the vegetable stimuli with simple shapes. When the colour-shape association was arbitrary, was there still an advantage for yellow form conjunctions?

Method

Participants

Eight right-handed students and employees at the University of Birmingham took part in the experiment (2 male, mean age 30). All participants had normal or corrected vision and gave informed consent approved by the School of Psychology, University of Birmingham.

Stimuli

Each of the four vegetable stimuli was replaced with a simple geometric shape (corn – square, carrot – circle, aubergine – vertically elongated rectangle, lemon horizontally elongated rectangle). For each of the twelve stimuli in Experiment 1 (four vegetables in three colours), the average colour was sampled from the centre of the image (excluding areas of extreme shading or light) and sampled over a square with a 5° radius. This mean colour was then applied to the corresponding geometric shape (see Figure 16, for an example), which was matched to size to the stimuli used in Experiment 1a.

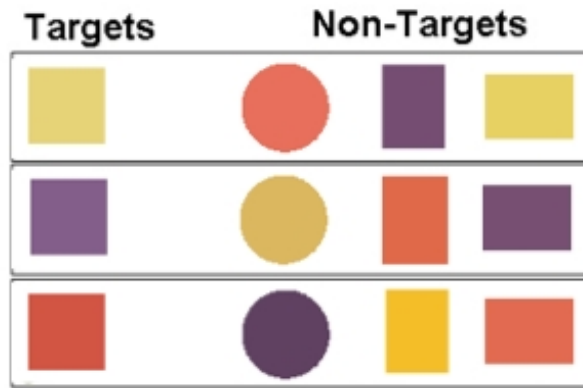


Figure 16: The stimulus pairings used in Experiment 1b.

Other than the stimulus modifications outlined above, the methodology was identical to Experiment 1a. Participants were asked to search for a target square, which could be in either of three colours.

Results and Discussion

Target present trials

In Figure 17 I present the data for search efficiencies (RTs/prop. correct) when participants detected yellow, orange or purple coloured target square. Search efficiency increased linearly as a function of display size ($F(2, 14)=63.73$, $p<0.001$). There was no reliable effect of the target colour ($F(2, 14)=1.52$, $p=0.252$) and target colour did not interact with the display size ($F<1.0$). The search rates for the three types were equivalent (yellow: 29 ms/item, orange: 27 ms/item, purple: 30 ms/item) and were certainly not uniquely efficient for yellow targets. For all targets the search was relatively slow, and consistent with a serial search (>40 ms/item). These findings indicate that the yellow corn in Experiment 1a did not pop-out because of its colour.

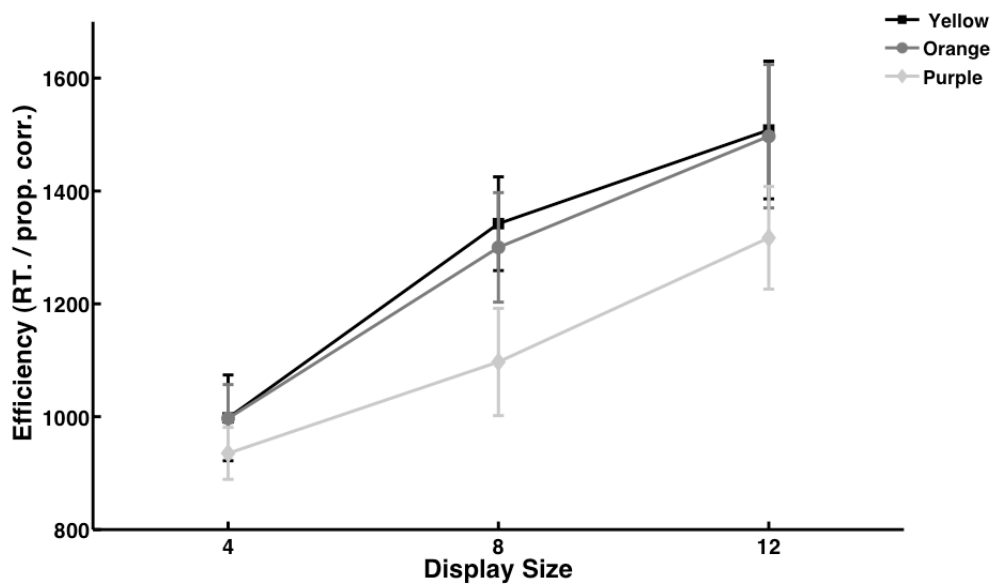


Figure 17: The mean efficiency (RT/prop. corr.) for search for geometric shape targets in yellow, orange and purple as a function of the different display sizes (4, 8 and 12) in Experiment 1b.

Target absent trials

Response efficiency on target absent trials is shown in Figure 18. The data are separated according to the set of non-target stimuli paired with each of the target types. Efficiency increased linearly as a function of display size ($F(2, 14) = 121.208, p < 0.001$). There was no main effect of non-target stimulus group ($F(2, 14) = 1.433, p = 0.272$) but this did interact with set-size ($F(4, 28) = 2.795, p = 0.045$). The interaction reflected small variations across the various non-target sets at the 3 display sizes, but there was no evidence for systematic effects of non-target colour on search and there were no significant differences between the non-target sets at any display size (4: ($F(2, 14) = 2.029, p = 0.168$), 8: ($F(2, 14) = 2.327, p = 0.134$), 12: ($F(2, 14) = 2.04, p = 0.167$)).

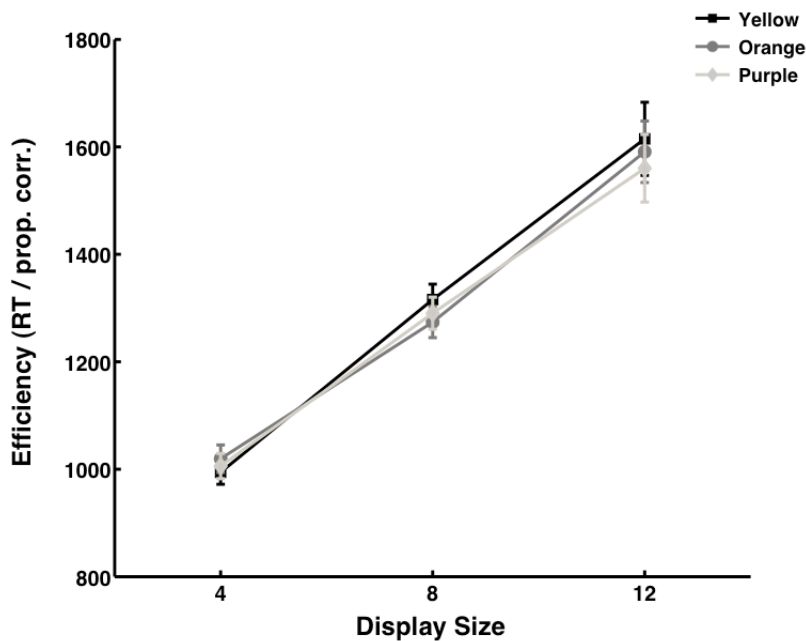


Figure 18: The mean efficiency (RT/prop. corr.) on target absent trials for geometric shapes (Experiment 1b). Non-target stimuli sets were divided according to the target pairings (yellow, orange and purple squares). Performance is displayed as a function of display size (4, 8 and 12).

The data from Experiment 1b indicate that there was no advantage in search slopes for yellow shapes (carrying the correct target colour from Experiment 1a) compared with shapes carrying the equivalent of an incorrect colour from Experiment 1a. Hence the efficient search for yellow over purple or orange corn was not by dint of its colour alone, as opposed to participants having stored knowledge of yellow as the colour of corn.

One difference between Experiment 1a and 1b is that, in Experiment 1a only, participants could draw on stored knowledge not only of the target but also the non-targets. Since targets and non-targets were both correct or both incorrect together, participants could use information from the non-targets to predict the colour of the target, and this might work most easily when the target and non-targets carried their standard colour. For example, having found an orange carrot, participants could predict that the target corn, when present, would be yellow. Experiment 1c was designed as a further control study to test this and to assess if it was critical whether the colour fell on the surface of the objects or not. Prior work on object identification has demonstrated that having the correct colour depicted can

facilitate object naming, but primarily when the colour falls on the surface of the objects; there can be little benefit when the colour falls in the background (Price & Humphreys, 1989). If the predictability of the target based on the colours linked to the shapes was critical here, then having the colour on the surface or the background of the individual object should not matter; the known target colour would be equally predictable once the known non-target colour is coded (detecting a carrot on an orange background would inform participants that the corn, when present, would be on a yellow background. Search could then be guided to yellow items, just as when the colour was on the surface of the objects). On the other hand, if the target detection depends on the activation of stored knowledge, which is sensitive to how the colour normally falls on the object's surface, then the advantage for the correctly coloured target should decrease when the colour falls in the local background of each shape. These predictions were tested here.

Experiment 1c: Effects with background colours

Method

Participants

There were 10 participants who were either postgraduates, post-doctoral fellows or members of staff of the Universities of Birmingham and Oxford. There were 6 females and 4 males and a mean age of 33 years. All had normal or correct-to-normal vision.

Design and Procedure

The Design and Procedure were exactly the same as in Experiment 1a except that each object was depicted in grey-scale and presented on a local coloured background. The background colours were extracted from the surface colours used in Experiment 1a and covered behind the stimulus so that each background subtended an area of $2.2^\circ \times 2.2^\circ$. In a prior study of object naming, Rappaport, Riddoch and Humphreys (sub, Chapter 4) showed that, when objects were shown with an incorrect colour, there was little difference in naming times for items where the colour was on the surface and those where it fell in the background suggesting that any reduced contrast, when the objects were presented on a coloured as opposed to a white background, did not have a major impact on object identification. Figure 19 illustrates the stimuli. Participants were told that each item was depicted against a background that could or could not match the object's colour in real life. They were also told that when the non-targets were presented on backgrounds that were the correct colours for those objects, then the target would fall on a background that was the correct colour for that object (yellow as opposed to purple or orange).

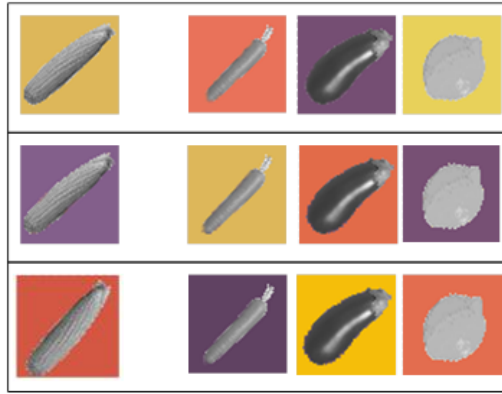


Figure 19: Example stimuli from Experiment 1c. The targets are shown on the left (corn) and the non-targets presented with each target are depicted in the same row.

Results and Discussion

Target present trials

The mean efficiency for search in each condition is illustrated in Figure 20. A two-factor repeated measures ANOVA was conducted with target colour (correct or incorrect) and display size as the factors. The effect of display size was highly significant ($F(2,18)=17.08, p<0.001$) but neither the main effect of target colour nor the target colour x display size interaction approached significant (both $F_s<1.0$). For objects depicted on either the correct or the incorrect background colour, search was very slow (60 and 66 ms/item respectively).

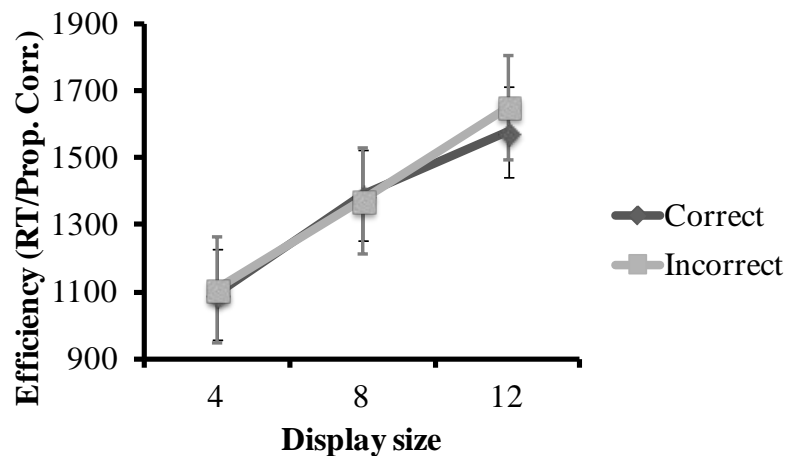


Figure 20: Target present trials in Experiment 1c, with objects depicted on backgrounds that were or were not the correct colours for the real stimuli

Target absent trials

The target absent trials were also separated according to whether the non-targets fell on backgrounds that were the correct or incorrect colour for each item. The mean efficiency of search in each condition is presented in Figure 21. There was a highly reliable effect of display size ($F(2,18)=52.05, p<0.001$) but the effect of target colour was not significant ($F(1,9)=3.10, p>0.10$) and neither was the target condition x display size interaction ($F<1.0$). The search slopes were 185 and 168 ms/item for correct and incorrect non-target displays.

In Experiment 1c search was again very slow and strongly affected by the display size. Critically, there was no effect of whether the background colour was correct or incorrect for the item. Participants were not able to use the colour of the non-targets to guide their search to targets depicted on the correct background colour despite having ample time to do this under the slow search conditions. The results indicate that the colour needs to be displayed on the surface of the object in order for an effect of the correct colour to emerge (in Experiment 1a), but the mere presence of the colour is not sufficient to modulate

performance. This is consistent with search being dependent on the bound colour-form stimulus.

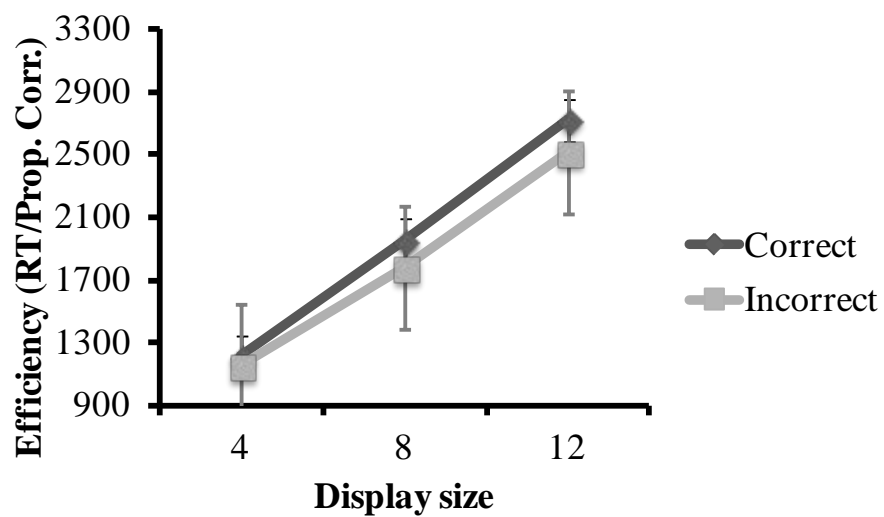


Figure 21: Mean efficiency of performance in Experiment 1c (background colours)

Experiment 2a: Non-Target Colour-Congruency Effects

In the previous experiments colour-shape pairings were consistent across targets and colour, such that correctly coloured target was always paired with correctly coloured distracters (or vice versa). Experiment 2a provided a further test of whether the non-target colour was critical to the advantage for correct target colours. Here I orthogonally manipulated whether the target or the non-targets were shown in their correct colour or in an incorrect colour, creating four types of display (target correct or incorrect x non-target correct or incorrect). The displays appeared randomly making it impossible for participants to predict the colour of the target on the basis of whether the non-targets were shown in their correct colour. Does the advantage in search efficiency for correctly coloured targets still occur? Moreover, I used different items to those used previously in order to generalise the effects across stimuli. To assess the effects of the different target colours per se, Experiment 2b was conducted in which the same colours were assigned to geometric shapes.

Method

Participants

Eight participants with normal / correct vision were recruited according to the same criteria as previous experiments (1 male, 2 left-handed, mean age: 33).

Stimuli

There were four pictures depicting colour-diagnostic items pepper, lime, plum and strawberry. Target pepper stimuli were rendered correctly in red and incorrectly in purple. Each non-target item was rendered in three different colours: green (diagnostic for lime),

purple (diagnostic for plum, and matching the purple pepper) and red (diagnostic for strawberry, and matching the red pepper). Colours were exchanged using the colour picker tool provided in GIMP 2.6 image manipulation software. All stimuli were presented on white equiluminant background were scaled to 57 x 57 pixels subtending approximately 1.8° x 1.8°. Examples are given in Figure 22.

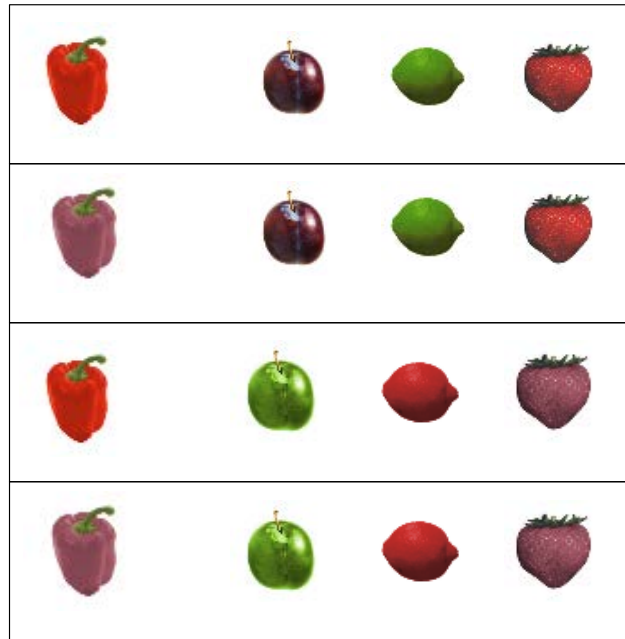


Figure 22: Example stimuli from Experiment 2a. The target is shown on the left of each figure and the non-targets appearing along with it are depicted along each row. Rows 1 and 3 correct target, rows 2 and 4 incorrect target. Rows 1 and 2 correct non-targets; rows 3 and 4 incorrect non-targets. The displays were selected at random.

Design and Procedure

Participants searched for a correctly (red) or incorrectly (purple) coloured pepper amid an array of four, eight or twelve stimuli. Again, a target was present on half of trials, and the target type appeared with equal probability. On half of the trials non-target items were correctly coloured and the other half they were all incorrectly coloured. Colour-shape congruency was therefore consistent across non-target items (i.e. all non-targets were either correctly or incorrectly coloured), but this was varied independently from the target colour. For half of the target present trials correctly coloured targets were accompanied by

correctly coloured distractors, and for the remaining trials they were accompanied by incorrectly coloured distractors. For each trial there were equal numbers of non-target purple, red, and green items. Participants separately completed two sessions of 720 trials, and the data is averaged across both.

Results and Discussion

Target present trials

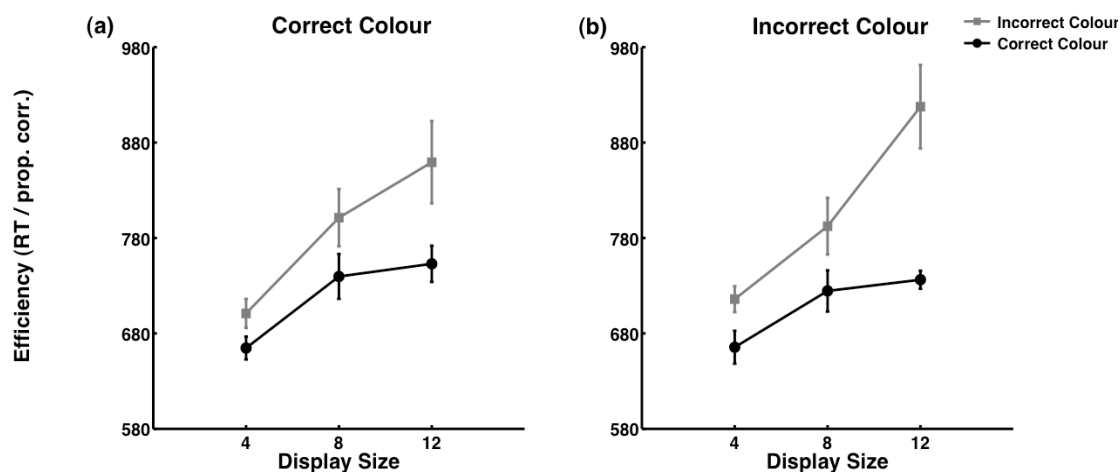


Figure 23: Experiment 3. The mean efficiency for search for correctly and incorrectly coloured targets according to whether the accompanying non-targets were correctly (a) or incorrectly (b) coloured (Experiment 2a).

In Figure 23 I present the data for search efficiencies (RT / prop. corr.) when participants detected red or purple target peppers. The results are separated according to the non-target colour-shape congruency. There were reliable effects of display size ($F(2, 14) = 23.8$, $p < 0.001$) and target colour ($F(1, 7) = 8.321$, $p = 0.023$) and these factors interacted ($F(2, 14) = 5.530$, $p = 0.017$, Figure 23). Search for correctly coloured targets was more efficient across the display-sizes and yielded a shallow slope consistent with a parallel search (9.5 ms/item). For incorrectly coloured targets the search was more than twice as slow (21.6

ms/item). This finding replicates that reported in Experiment 1, extending these conclusions to a different stimulus set.

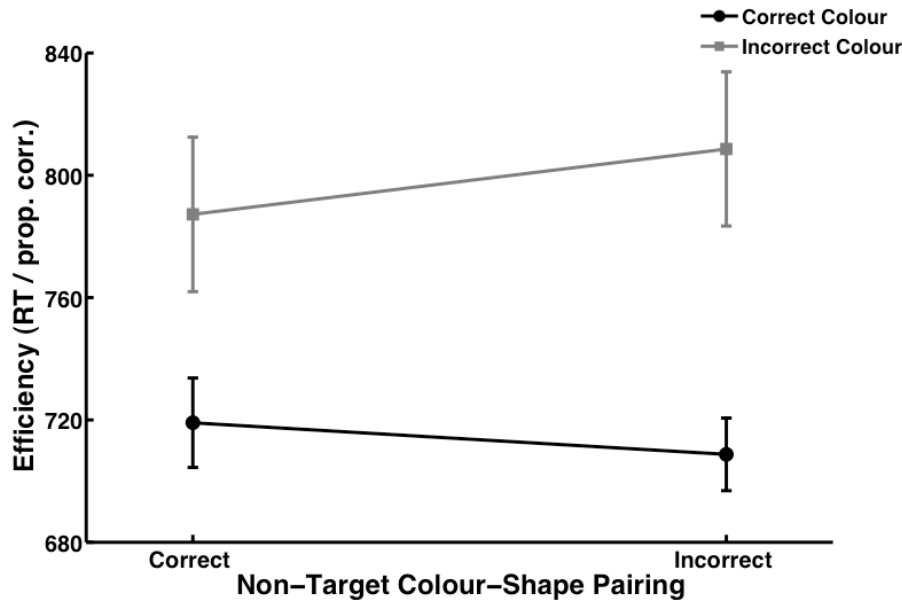


Figure 24: Search efficiency averaged across the three display sizes. Non-target colour-shape pairing is displayed on the x-axis, and performance is separated according to the appropriateness of the target colour (Experiment 2a).

Target and non-target colour-shape pairing also significantly interacted ($F(1, 7) = 10.307$, $p = 0.015$, Figure 24). Correctly coloured targets were always detected more efficiently than incorrectly coloured targets. For both target-types, detection was most efficient when non-targets carried out the opposite colour relations to targets. That is, search for correctly coloured targets was faster when the non-targets were coloured incorrectly, while search for incorrectly coloured targets was faster when the non-targets were coloured correctly. The three-way interaction between all the factors did not reach significance ($F(2, 14) = 3.168$, $p = 0.073$ n.s.).

Target absent trials

Target absent response efficiency was analysed using a repeated measures ANOVA including non-target type (correctly or incorrectly coloured), display size (4, 8, 12) as

factors. There was a main effect of display-size only ($F(2, 12) = 25.121, p < 0.001$, all other F 's < 4).

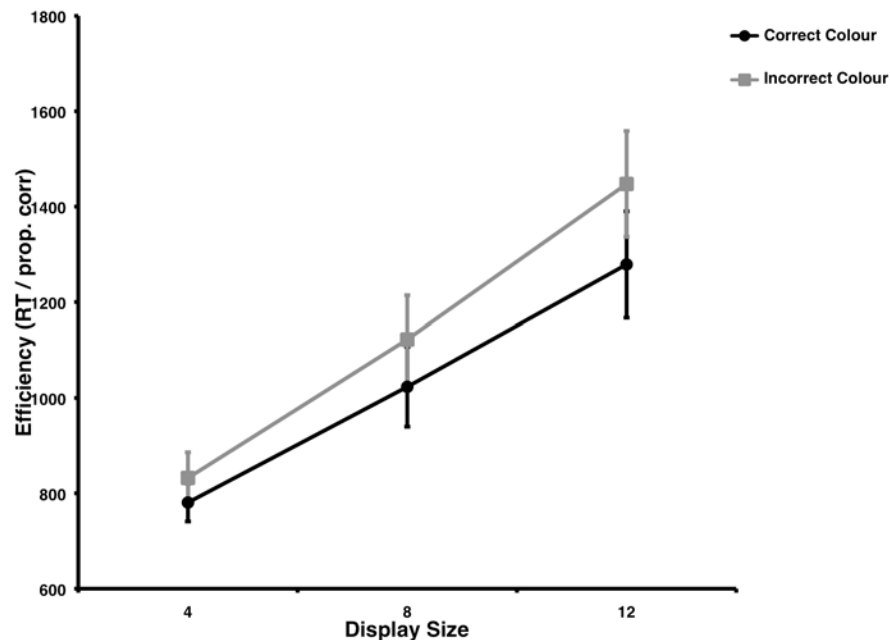


Figure 25: Mean search efficiency target absent trials as a function of the colours of the non-targets (Experiment 2b)

The data from Experiment 2a support those from Experiment 1c in showing efficient search for targets carrying their correct colour relative to the same targets presented in an incorrect colour, under conditions in which search for the latter stimuli was inefficient. This result occurred even when the non-target stimuli randomly carried their correct or incorrect colours, so that participants could not anticipate the likely colour of the target after detecting that a non-target was in the correct colour. In this case, the advantage for correctly coloured targets cannot be attributed to participants using the non-targets in familiar colours to predict the target colour. Indeed, search for a correctly coloured target was fastest in the condition in which the non-targets were in their incorrect colour, whilst the detection of an incorrectly coloured target was slowest in this case (Figure 24). These data can be explained if there is efficient guidance of search to stimuli presented in their

correct colour, relative to when the same items appear in incorrect colours. When the target is correct and the non-targets incorrect, attention is guided efficiently to the target since the non-targets are less strong competitors for selection. When the target is incorrect, search is relatively slow due to the competition from non-targets sharing similar features. The slow search is helped when non-targets are correctly coloured because these items can be selected and rejected relatively efficiently compared to when the same items are coloured incorrectly. The results are that opposite effects of non-target colour emerge on the detection of correct and incorrectly coloured targets.

Experiment 2b: Assigning the colours to geometric shapes

Although the data from Experiment 2a fit again with the idea that attentional limitations on selection are reduced when a target carries its familiar colour, it remains the case that the correct and incorrectly coloured targets carried different colours. It could again be that items in red (the correct colour in Experiment 2a) are search for more efficiently than items in purple (the incorrect colour in Experiment 2a), and this underlies the observed differences in search efficiencies. To test this, Experiment 2b used the same colours as Experiment 2a but I now assigned them to geometric shapes (following Experiment 1b). Was there still an advantage for ‘correct’ (red) over ‘incorrect’ (purple) distractors?

Method

Unless otherwise mentioned the Method was the same as for Experiment 1b.

Participants

Eight right-handed students and employees at the University of Oxford took part in the experiment (2 male, mean age 32). All participants had normal or corrected vision and gave informed consent approved by the local research ethics committee.

Stimuli

Each of the objects in Experiment 2a was replaced with a simple geometric shape (pepper – circle, plum – triangle, lime – horizontal oval, strawberry vertical oval). For each of the stimuli in Experiment 2a the average colour was sampled over a central square with a 5° radius. This mean colour was then applied to the corresponding geometric shape (see Figure 25, for an example), which was matched to size to the stimuli used in Experiment 2a.

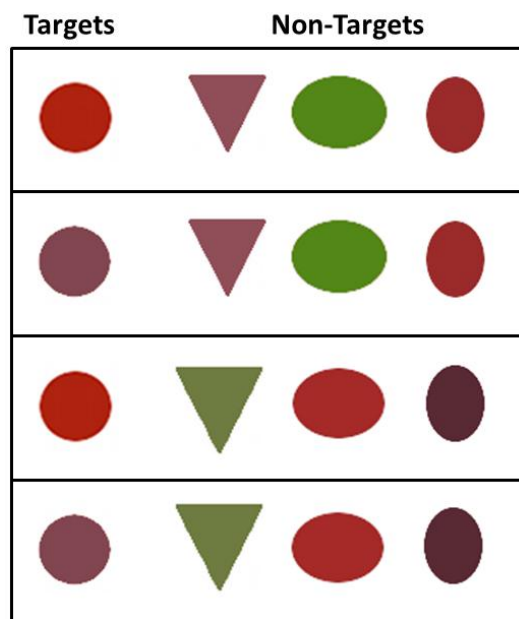


Figure 25: The stimulus pairings used in Experiment 2b. The target was either ‘correct’ (red) or ‘incorrect’ (purple), and the non-targets were arbitrarily coded as ‘correct’ (top two lines; red and green ovals) or ‘incorrect’ (bottom two lines; red and purple ovals).

Other than the stimulus modifications outlined above, the methodology was identical to Experiment 2a. Participants were asked to search for a target circle, which could be in either red or purple, and the two sets of non-targets (carrying different colours) appeared randomly paired with either target, on target-present trials.

Results and Discussion

Target present trials

The efficiency data were analysed in an ANOVA with target colour (red, purple), non-target set and display size (4, 8, 12) as within-subjects factors. All the main effects were reliable (target colour: $F(1,7)=7.14$, $p<0.05$; non-target set: $F(1,7)=18.22$, $p<0.01$; display size: $F(2,14)=22.20$, $p<0.001$). None of the interactions approached significance (all $F<1.0$). Performance overall was more efficient when the target was red, with the first rather than the second non-target set (red and green ovals vs. red and purple ovals), and with small rather than large display sizes. However, the effects of display size did not vary as a function of the target colour of the distractor set. The data are shown in Figure 27.

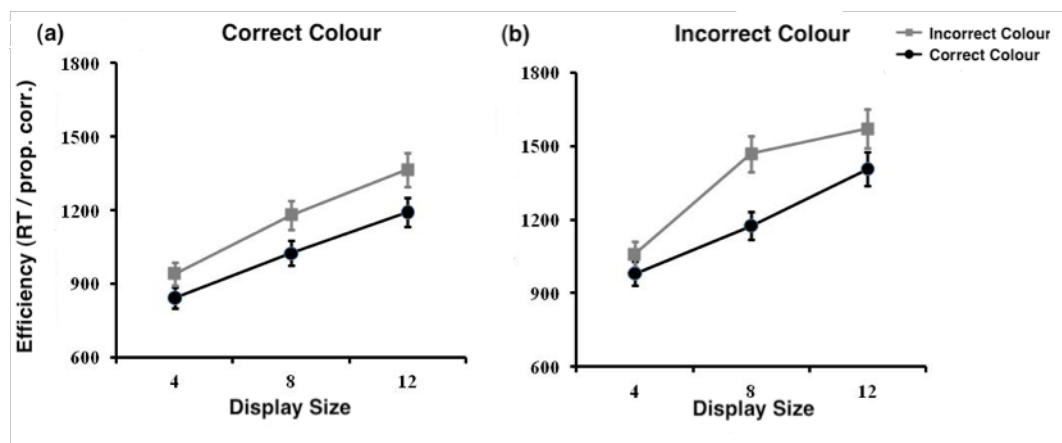


Figure 26: Efficiency scores for search for correct (red) or incorrect (purple) coloured targets as a function of the colour of the non-targets ((a) correct – red and green ovals; (b) incorrect – red and green ovals) (Experiment 2b). Error-bars represent standard error of the mean.

Target absent trials

A two-factor repeated measures ANOVA was conducted with the factors being non-target colour ('correct'[red and green ovals and purple triangle], 'incorrect' [red and purple ovals and green triangle]) and display size (4, 8, 12). There was a highly reliable effect of display

size ($F(2, 14)=119.38$, $p<0.001$) and non-reliable trends for effects of non-target colour ($F(1,7)=3.61$, $p=0.10$) and a non-target colour \times display size interaction ($F(2,14)=2.68$, $p=.10$). Performance tended to be more efficient overall, and to increase less with display size, when the non-targets were ‘correct’ in colour.

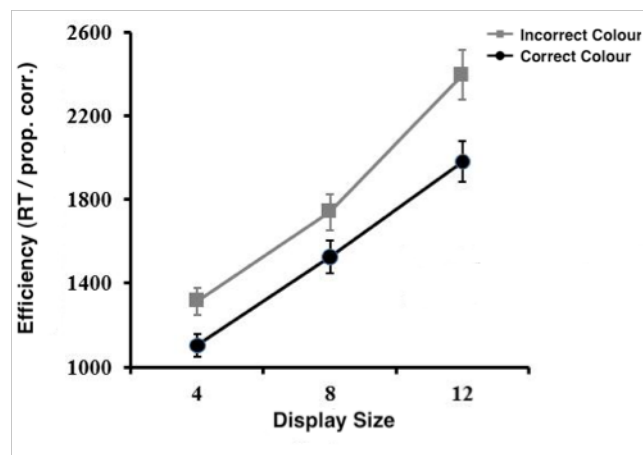


Figure 27: Mean efficiency scores on target absent trials as a function of the colours of the non-targets (Experiment 2b). Error-bars represent standard error of the mean.

The data indicate that there was an overall advantage for detecting red vs. purple distractors, and also that the particular set of non-targets affected performance. This last result likely reflects two factors: (i) the greater similarity to the target of the oval non-targets compared with the triangle non-target, and (ii) that the oval non-targets were less similar in colour to the target in the ‘correct’ set (red and green ovals) than in the ‘incorrect set’ (red and purple ovals). However, critically, neither of these factors interacted with the display size. That is, the efficiency of the search process was not modulated by the target’s colour and, for both red and purple targets, search was highly inefficient (49 and 59 ms/item respectively). The overall advantage for red compared with purple targets may arise because the red circle was easier to identify once selected, or because there was a bias to respond present to red compared to purple items. Whichever is the case, there was no support for the idea that the advantage in the efficiency of search for red over purple peppers (Figure 27), in Experiment 2a, was due to their colours.

Experiment 3: High probability incorrectly coloured targets

In the third experiment, I examined whether the efficient selection of correctly coloured targets reflected a top-down set adopted by participants when told to look for a familiar target. It is possible that holding a template for a familiar item ('corn') may activate all of its related features (its colour but also its familiar sound, the representations of semantically related items etc.), and all of these attributes may be used to form the top-down expectancy for the target. Previous studies have shown that visual localisation and search can be modulated by the presence of congruent stimuli associated with an expected target. For example, Iordanescu et al. (2008) reported improved target localisation when a congruent sound was presented at the same time as target stimuli (hearing a 'miaow' helped participants localise a cat). Moores et al. (2003) found that search was affected by the presence of a non-target semantically related to the target and this has been shown to modulate the initial orienting of attention in search display, measured using ERPs (Telling et al., 2010). In Experiments 1a and 2 here participants may have carried an expectation weighted for the correct target colour across the experiment (target corn = 'expect yellow'), facilitating the selection of the correctly coloured target (e.g., by top-down activation of the expected colour map; Wolfe, 1994). In Experiment 3 I altered the probabilities with which targets appeared in their different colours, with presentations biased to an incorrectly coloured target (the target, corn, was the incorrect colour purple on 67% of the trials and the correct colour, yellow, on only 33% of the trials). Under these conditions, participants should adopt a top-down set of searching for a purple rather than a yellow target. Does this top-down set now overrule the advantage for correctly coloured targets? As well as measuring reaction times and accuracy I also examined eye movements to provide a direct analysis of any expectancy-bias to targets of a particular colour. Of particular interest is the pattern of eye movements on trials when the target is

absent (i.e., when no target is present to compete for selection with the non-targets). Are first eye movements made to non-targets carrying the familiar colour associated with the target (yellow), or are they directed to non-targets carrying the likely colour of the target (purple)? Evidence for first eye movement to purple non-targets would provide an index that participants did adopt a top-down set to the incorrect (but more probable) target colour.

Method

Participants

Twenty participants were recruited all with normal or correct-to-normal vision (2 male, 2 left handed, mean age: 27). Eye-movements were recorded during the task for seven of these participants.

Apparatus

Eye-movements were recorded using Eye-Link II with a spatial resolution of 0.01° and a temporal resolution of 2-4 milliseconds. Eye-movement calibration was performed prior to each experimental block, and was subject to drift correction on each trial prior to trial onset. Fixations were recorded when the eyes did not exceed a velocity threshold of $30^\circ/\text{sec}$, an acceleration threshold of $8000^\circ/\text{sec}/\text{sec}$, or a motion threshold of 0.1° and the pupil was not missing for more three or more samples in a sequence.

Design and Procedure

The methodology in Experiment 3 was identical to Experiment 1a with the exception that only yellow and purple corn targets were presented (along with their respective non-targets; Figure 12). Yellow corn targets had low prevalence, occurring on just 33% of

target-present trials, while purple corn targets appeared on 67% of target-present trials. Participants were told these probabilities.

The procedure used during eye-movement recordings was identical to the behavioral task outlined above with the following exceptions: Participants completed four rather than five blocks (reflecting the extra time required for calibration when eye movements were recorded). In addition the minimum inter-item-distance was increased from 70 to 100 pixels to ensure that fixations to an item were unambiguous.

Results and Discussion

Target present trials

The efficiency of search (RT/prop. correct) on target present trials is shown in Figure 28 according to whether the preceding trial had a target with the same colour, a different colour or no target. Search was overall more efficient than in Experiment 1a, which used the same stimuli, likely due to the greater inter-item separation and perhaps also the lower weighting given to the non-target colour orange (never a target colour). Despite the greater likelihood of targets appearing in the incorrect relative to the correct colour, search was more efficient for correctly coloured targets relative to incorrectly coloured targets, and, based on RTs alone, the slopes were respectively 5 and 11 ms/item (if we discount orange coloured non-targets when calculating slopes then the search rates were 11 and 22 ms/item). Based on measures of search efficiency, the slope advantage for correct over incorrectly coloured targets held when the preceding trial had no target ($F(2,38)=14.50$, $p < 0.001$) and when there was a target in a different colour ($F(2,38)=3.97$, $p = 0.027$). There remained a marginal advantage even when the preceding trial had a target with the same colour ($F(2,28) = 2.84$, $p < 0.10$) (Figure 28).

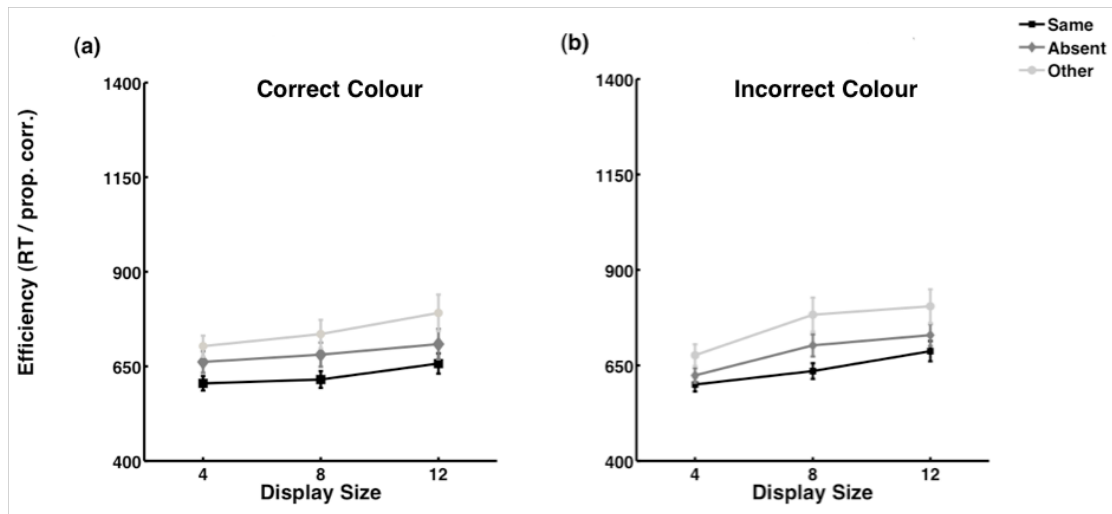


Figure 28: Experiment 3: The mean efficiency (RT/prop. correct) for search for correctly coloured targets (a) and for incorrectly coloured targets (b), when there was a presentation bias favouring the incorrectly coloured targets. Performance is shown as a function of the preceding trial: target same colour, target different colour, target absent. Error-bars represent standard error of the mean.

Target absent trials

Target absent data are shown in Figure 29. A repeated measures ANOVA was conducted with non-target type (correctly or incorrectly coloured). There was a main effect of display-size ($F(2, 20) = 82.74, p < 0.001$) and this factor had a borderline interaction with non-target type ($F(2, 38) = 2.82, p = 0.072$). Response efficiency on trials with correctly coloured non-targets were higher than those on trials with incorrectly coloured non-targets for display size 8 (782 vs. 807 ms/prop. correct; $p < 0.05$ Bonferroni test), while there were no differences at the other display sizes (Figure 29).

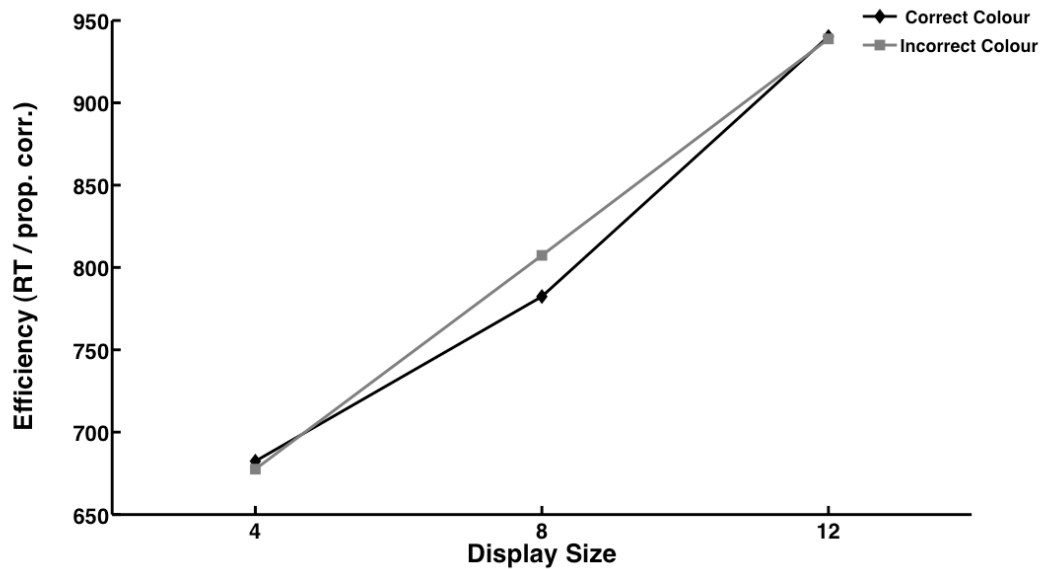


Figure 29: Target absent response efficiency is shown as a function of display size, and is separated according to the appropriateness of the target colour (correct or incorrect; Experiment 3). Error-bars represent standard error of the mean.

To quantify expectancies during search, I analysed the number of first-fixations per stimulus type. In addition, to measure processing and selection efficiency I analysed the average fixation duration within a region (the dwell time) and the frequency of fixations to a target within a trial. These measures are considered separately for target and non-target items.

First Fixation

i) Target Items

A repeated measures ANOVA of first fixations to targets revealed that significantly fewer first-fixations were made to correctly coloured relative to incorrectly coloured items ($F(1, 6) = 9.991, p = 0.02$). There was no effect of display size ($F(2,12)=0.646, p=0.542$) and no interaction ($F(2,12)=0.911, p=0.0428$).

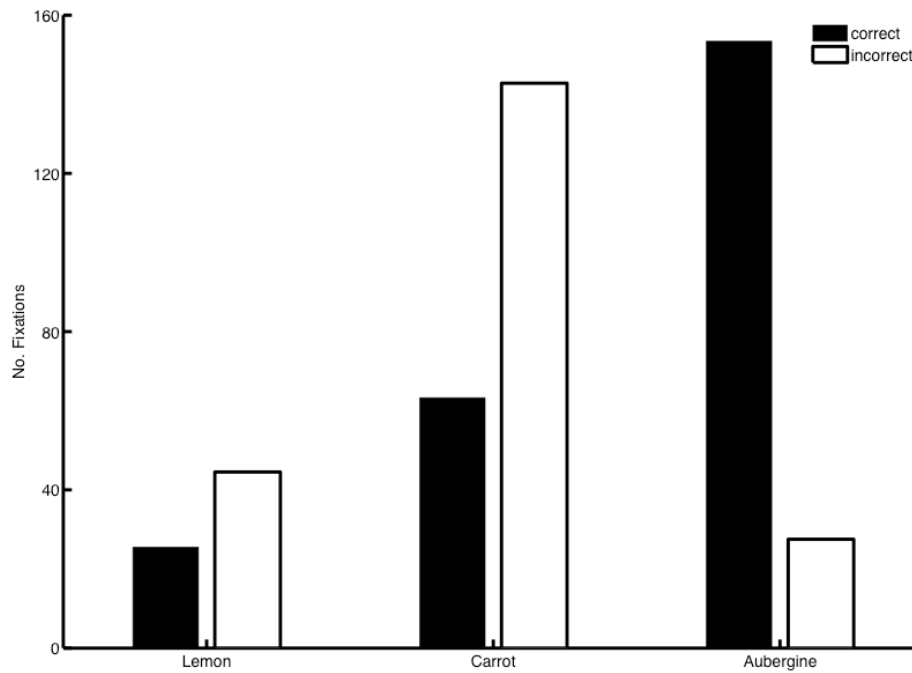


Figure 30: The number of fixations to the different coloured items, summed across absent and present trials, scaled for the different proportions on trials for correct and incorrectly coloured targets. The lemon could be yellow (correct) or purple (incorrect). The carrot could be orange (correct) or purple (incorrect). The aubergine could be purple (correct) or orange (incorrect). Performance here is averaged across the display sizes (Experiment 3).

ii) Non-Target Items

Figure 30 shows the number of first fixations, averaged across the display sizes, to the 3 types of non-target. Most fixations were to the carrot, next to the aubergine and then the lemon, reflecting shape similarity to the target (corn). To assess the effects of non-target colour on performance, I measured first fixations to the carrot and aubergine (the non-target shapes most similar to the target) when they carried the potential target colours (yellow and purple). Our measure here was normalized by fixations to the same items when they were orange, since this provides a measure of shape similarity when the carrot and aubergine non-targets had the same colour (in Figure 30 the relevant data are in the columns ‘carrot correct’ and ‘aubergine incorrect’). The normalized ratio of fixations to the aubergine when purple relative to the carrot when yellow was at least 2:1 (the ratio of fixations did not differ from 2:1 averaging across the display sizes; $t < 1.0$, $p = .393$; Figure

31). This ratio matches the prior probabilities of the purple and yellow corn targets (the purple corn target being twice as likely here). This last result was not due to the aubergine and carrot respectively being the correct and incorrect colours in this comparison, as there were more fixations to the (incorrect) purple than the (correct) yellow lemon non-target ($F(1,6)=19.57$, $p<0.01$), and this ratio did not differ from 2:1 ($t<1.0$, $p=.678$). These results indicate that first fixations on target absent trials closely following the likelihoods of the target colours. This in turn demonstrates that participants had expectancies favouring the incorrect target colour. It follows that top-down guidance of search should direct attention first to purple stimuli, prior to the search of any yellow items, leading to stronger effects of display size on the correctly coloured yellow corn targets. Despite this, search was more efficient for targets in the correct colour.

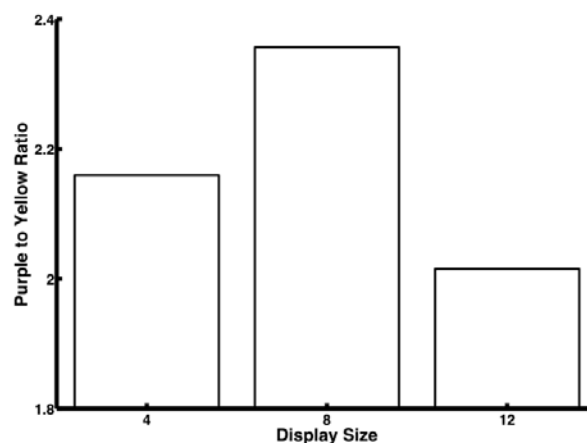


Figure 31: The ratio of fixations on purple relative to yellow color non-targets (carrots and aubergines), normalized by the fixations to both non-targets when they were orange (a measure of the shape similarity of each non-target to the target). The ratio of first fixations to purple rather than yellow non-targets was approximately 2:1

Fixation Durations

For each participant an outlier analysis was performed to remove trials where the fixation duration exceeded 2.0 standard deviations above and below the mean. The data were analysed for purple and yellow non-targets only (there were too few to assess fixation durations to orange non-targets).

i) Target Items

There was a significant main effect of target colour ($F(1, 6) = 51.83, p < 0.001$). Fixation durations were significantly longer to targets that were coloured correctly (mean: 215 ms) relative to targets coloured incorrectly (mean: 207 ms, Figure 32). There was also a main effect of display-size ($F(2, 12) = 4.91, p < 0.05$), but this did not interact with target colour ($F(2,12)=2.001, p=0.178$).

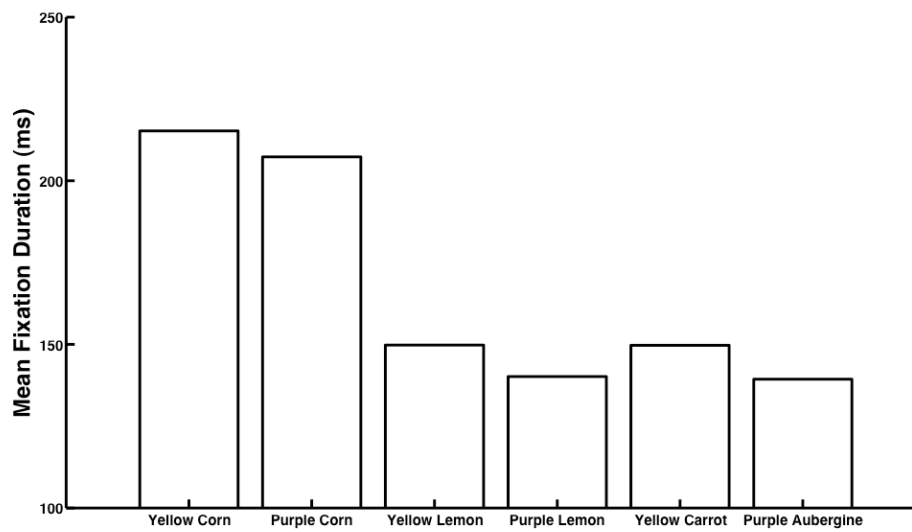


Figure 32: Mean fixation durations (dwell time) to stimuli carrying a target colour (yellow or purple).

ii) Non-Target Items

Fixation durations to carrot and aubergine non-targets, when presented in potential target colours (yellow, purple), were averaged across target present and absent displays. There was a main effect of colour ($F(1, 6) = 25.71, p = 0.002$); participants fixated longer on yellow carrot non-targets. A significant effect of display-size was also found ($F(2, 12) = 35.45, p < 0.001$); participants tended to dwell longer on non-target items at small display sizes. The same analysis was conducted for lemon non-targets. There were no significant effects or interactions (all F 's < 2).

Target Re-Fixations

Finally, the average numbers of fixations to targets were also calculated for each trial. There were fewer fixations to correctly coloured targets than to incorrectly coloured targets ($F(1, 6) = 51.42, p < 0.001$, Figure 33), and more re-fixations to all targets as the display size increased ($F(2, 12) = 4.75, p < 0.05$). The results suggest that it took longer to recognise an incorrectly coloured (purple) target than a correctly coloured (yellow) target, so that more re-fixations were required. This occurred even though a greater number of first fixations were directed towards purple stimuli, reflecting the likelihood that the target was purple.

The RT and error data indicate that search was more efficient for correctly coloured (yellow) than incorrectly coloured (purple) targets, and correctly coloured non-targets also tended to be easier to reject (on target absent trials). In contrast to this, the eye movement data indicated that participants tended to direct their first fixations to stimuli carrying the non-target colour (purple), consistent with a top-down bias to search for a purple target. The search advantage for yellow targets occurred despite participants adopting an opposite top-down bias when directing eye movements.

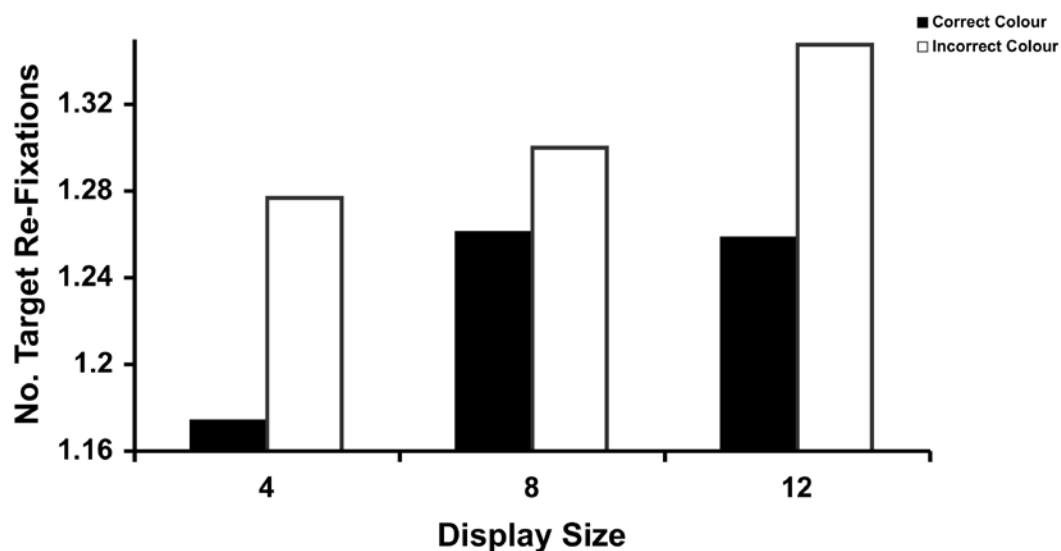


Figure 33: Mean number of re-fixations within a trial to correctly and incorrectly coloured targets as a function of the display size

General Discussion

The current data show that, under circumstances in which stimuli in arbitrary colours are not searched efficiently, there is efficient selection of targets in the correct colour, with the search rate difficult to reconcile with a biologically plausible serial search process (Experiments 1a, 2, 3). This advantage in search efficiency for correctly coloured targets was not due to the colour of the familiar targets being more salient than the other colours, since I found no effects of the target colour on search slopes in two control experiments using geometric shapes (Experiments 1b and 2b). The advantage for correctly coloured targets also seems unlikely to be due to participants anticipating the target colour from the colour of non-targets. In Experiment 1c I presented the same stimuli but as grey-level images on backgrounds that could be the correct or incorrect colour for the stimuli. As in Experiment 1a, correctly coloured targets were always paired with correctly coloured non-targets and vice versa, so that in both Experiments 1a and c, participants could predict the colour of the familiar target after detecting that a non-target had the correct colour. Moreover, in Experiment 1c participants were told of the relations between the target and non-target stimuli, and the slow search times in the study gave participants plenty of opportunity to identify a non-target and then to predict the target's colour from that. Search should then gain from attentional guidance to the target's colour. Despite this, there was no advantage for correctly coloured targets in this experiment. The data indicate that the colour had to be on the surface of the stimuli to generate efficient search. In addition, Experiment 2 replicated the effects using a different stimuli set when the colours of the non-targets was combined orthogonally with the colours of the targets making it impossible to predict the colour of the target from the non-targets. Although the non-targets carried no information about the target colour, search remained efficient for correctly coloured targets. Furthermore in Experiment 3 I demonstrated that search for

familiar colour-form conjunctions remained uniquely efficient even when these stimuli had a low likelihood of occurrence and participants had an expectancy bias to search for a target in a particular incorrect colour – indicated by eye movements being guided more frequently to purple than yellow non-targets on target absent trials.

These findings are consistent with previous experiments demonstrating that, in natural scenes, processing may advance to a high level without being strongly limited by attention (Potter, 1975, 1976; Li et al. 2002; Van Rullen and Thorpe, 2002). Researchers have distinguished between the processing of meaningless geometric shape stimuli and rich scenes filled with familiar detailed items, arguing that the later are “intrinsically superior” (Braun, 2003 pg. 8) and may be ‘hard-wired’ (Van Rullen, 2009). This conflicts with accounts such as Feature Integration Theory (FIT), where processing capacity is limited and attention is required for binding object features. Proponents of Feature Integration Theory however have questioned whether non attention-demanding conjunction coding is shown by studies showing apparently efficient detection of complex stimuli in scenes. These proponents argue that efficient detection can be explained by the processing of multiple unbound features, which, if sufficiently elaborate and unique, allow for target detection but not identification and localisation (Evans & Treisman, 2005). This argument is possible because the studies lack baseline conditions where the same features are present but are combined in an arbitrary manner. In contrast to these results, I show that, in baseline conditions, search was inefficient when displays had the same shapes and colours but the colours were assigned incorrectly to the shapes. This demonstrates that the presence of the features alone was not sufficient for targets to be discriminated efficiently. It is only when the objects carried the correct features on their surface that they ‘popped out’ in search. Our evidence is difficult to reconcile with a ‘multiple parallel *feature detection*’ idea, as familiar targets were defined only by their unique conjunction of features in the

array. This goes to the heart of theories such as FIT, where features need to be bound before activating stored perceptual representations and this binding process is held to be inherently limited by spatial attention. The data indicate that, while attentional limitations may hold for targets defined by arbitrary conjunctions of features, they hold much less for learned conjunctions. We need to re-conceptualise accounts of the binding process to take the critical effects of learning into account.

CHAPTER 6

THE UNCONSCIOUS BINDING OF LEARNED COLOUR- FORM RELATIONS: EVIDENCE FROM EXTINCTION

Synopsis

I report two experiments examining the effects of familiar colour-form relations on the effects of stimulus similarity on extinction. In a task requiring perceptual report of object identities I found that extinction was reduced if items with different shapes also had the same colour. This effect was particularly strong, however, when the colour-shape relations were familiar. The effect was not carried by whether the ipsilesional stimulus was correctly coloured or not, but reflect instead stronger grouping when both items have familiar colours. These data indicate that colour-form relations can be bound pre-attentively, contradicting current theories of human visual attention.

Introduction

Visual extinction is a relatively common neurological disorder following unilateral brain damage, classically associated with damage to posterior parietal cortex (Chechlacz et al., in press; Karnath et al., 2004). As discussed in Chapter 2 and 3, it is revealed behaviourally by successful detection of a single contralesional item but failure to detect the same stimulus when it is accompanied by a more ipsilesional stimulus. As the difficulty with contralesional stimuli manifests only in the presence of a competing ipsilesional item, extinction can be considered as a pathological bias in the normal competition for selection (Duncan & Humphreys, 1992; Duncan, Humphreys, & Ward, 1997). Within this framework the contralesional item has a reduced capacity to capture attention and consequently the ipsilesional stimulus is assigned the greater selection 'weight', winning the competition and reaching awareness.

Despite the poor awareness shown to contralesional items under bilateral presentation conditions, there is evidence that extinction can be mediated by the similarity of the contra- and ipsilesional stimuli. Effects of low-level grouping on extinction have been reported using an extensive range of factors including common colour, surface polarity, brightness and enclosure (Ward, et al., 1994; Gilchrist et al., 1994, Mattingley et al., 1997. See Chapters 2 and 3 for an overview).

Other work indicates that grouping effects on extinction are not confined to low-level properties of stimuli but can also be influenced by stimulus familiarity. Ward et al. (1994), for example, reported that, relative to when a vertical contralesional line was presented, there was reduced extinction for a horizontal contralesional line that could be grouped into an arrow with an ipsilesional bracket ($- > \text{vc. } | >$). This occurred even though the horizontal

line and the bracket did not share low level features. Using letters, Kumada and Humphreys (Kumada & Humphreys, 2001) also found less extinction when the contra- and ipsilesional items formed a word (g o) than when they formed a non-word (o g), despite low-level grouping being equated for such stimuli. They also demonstrated that the high-level 'lexical' grouping interacted with low-level grouping. For non-words extinction increased when the letters differed in contrast polarity compared to when they had the same contrast polarity, whilst the effects of contrast polarity were eliminated with words.

One account of extinction effects in patients is that it reflects poor binding of the features of contralesional items, exacerbated when attentional resources are reduced by the presence of the competing ipsilesional stimulus (Baylis et al., 1993, 2001). In particular, poor binding of the features to their location can lead to poor perceptual report. It has also been noted that patients showing extinction can also be poor at reporting conjunctions of colour and form, consistent with the patients having problems in binding together visual features (e.g., Humphreys, Hodson & Riddoch, 2009). Whether the problems in binding are confined to explicit perceptual report tasks, however, is unknown. I examined this in the present study, focusing particularly on whether there was binding of learned colour-shape relations when stimuli fall in the contralesional hemispace of patients showing visual extinction. The effects of binding were examined in an implicit procedure, in which the identity but not the shape-colour properties of stimuli had to be reported. I manipulated whether items presented on the ipsi- and contralesional sides of space shared the same or different identity and/or colour, and therefore whether the items grouped in the basis of their low-level principles. In addition, I varied whether the colour and shape of individual stimuli were familiar (e.g. yellow banana) or not (e.g. blue banana). I asked whether there were effects of colour similarity on extinction when shape identity was reported. Previously Baylis and colleagues (e.g., Baylis, Driver & Rafal, 1993; Baylis et al., 2001)

have argued that effects of colour and shape similarity on extinction arise when the colour or shape is relevant to the task, but not when the task is to report a different attribute (e.g., there is no effect of colour similarity when the task is report shape). Here, however, the shapes could have learned relations to the colour. Did the presence of this learned relationship modulate grouping and did any effects occur even when colour report was not required? Current theories of human visual attention propose that the binding of colour and shape is dependent on a first step in which attention is allocated to stimuli (Treisman, 1998). According to this account, patients with impaired attention to the contralesional side should be impaired at colour-form binding irrespective of whether the binding is learned or arbitrary, and hence there should be no evidence for grouping based on the colour-form conjunctions presented on the contralesional side. Evidence that there are effects of colour similarity on extinction, and that these effects are mediated by whether colour and shape form a familiar pairing, would contradict this proposal since, to enter into grouping, the shape and colour would need to be bound in the first place. I report two experiments demonstrating this. I examined perceptual report of object identities in patients showing extinction when the shapes of the objects were the same and then they differed. When the shapes are the same I expect that extinction should be reduced relative to when the shapes differ (cf. Gilchrist et al., 1996; Ward et al., 1994). Shape similarity may be sufficient to raise perceptual report of the contralesional item to a high level. Our interest then focused on report when the shapes of the contra- and ipsilesional items differed. Did colour similarity then modulate performance and were the effects dependent on the shapes carrying their learned colours?

Case Histories

Seven patients who had suffered a stroke and exhibited visual extinction took part in the experiments. Extinction in the patients was independently confirmed in a study requiring the patients to report two different letters (A-D, each 1 x 0.5 deg high and wide) presented for 200ms either alone 3 deg to the left or right of fixation or bilaterally in the same locations. Control participants made few errors under these conditions. The patients all showed significantly worse report of the contralesional item under bilateral relative to unilateral presentation conditions. Four of the patients had damage including inferior posterior parietal cortex on MRI scan (JB, PM and RH) and one had clinical symptoms in word finding and verbal short-term memory consistent with this (patient DB for whom no MRI scan was available). The other three (AS, DT and JW) had damage outside posterior parietal cortex but nevertheless showed visual extinction (non-parietal patient extinction previously noted by Duncan, 1998). In 4 patients (AS, JB, JW and PM) there was evidence of bilateral damage (Figure 34), but extinction was still clearly manifest on one side of space. This side, derived from the independent letter report task, was designated the contralesional side for the subsequent analyses. Reconstructions of the available lesions from MRI scans are shown in Figure 34 (neurological convention).

Six of these patients (AS, DB, DT, JW, PM and RH) took part in Experiment 1, and five in Experiment 2 (AS, DB, PM, JB and RH).

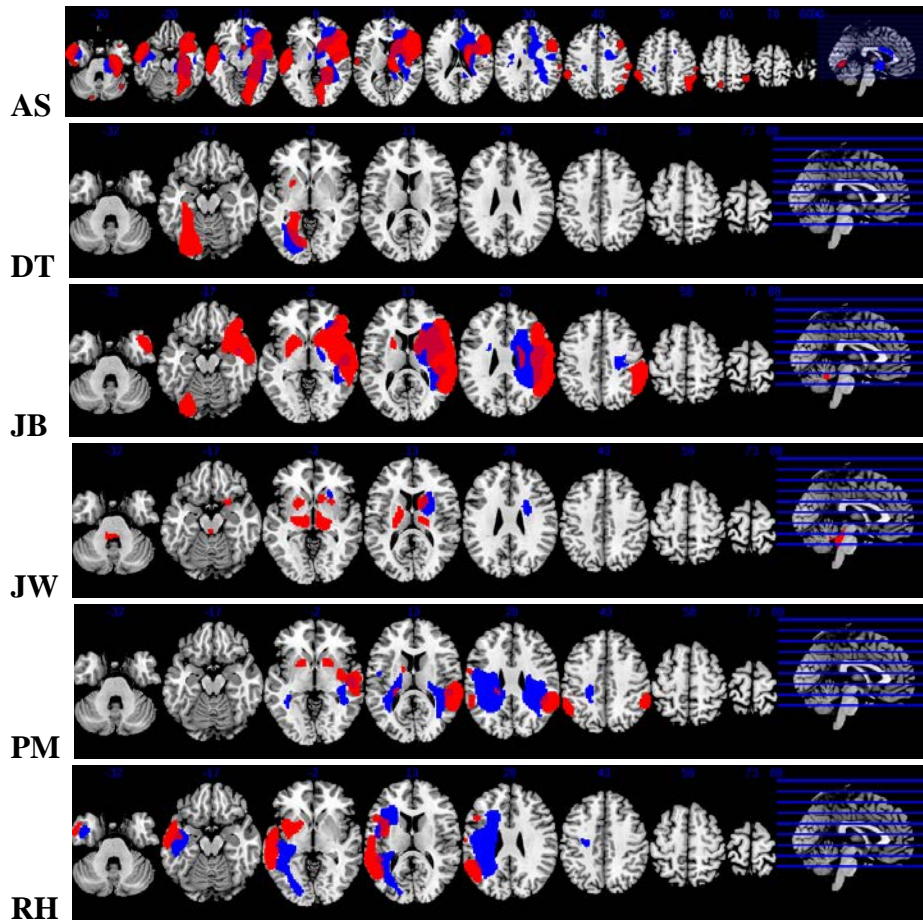


Figure 34: Lesion created using VBM analysis of T1 scans using a one-sampled t-test in SPM. This included 3 covariates: age, gender, acquisition location (BUIC / OASIS) healthy (209, age range 40-87) vs. patient. Sites showing a significant change in image intensity relative to the controls (FWE 0.001, >100 voxels) are rendered on a standard template in MRICron where red indicates grey matter and blue white matter damage. Scans were not available for DB.

Experiment 1: Effects of physical and learned colour

Materials and Methods

Apparatus

Observers viewed stimuli on a LG monitor ($\sim 26^\circ \times 33^\circ$) seated centrally approximately 65cm from the display. Stimulus presentation was controlled using MatLab and psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Stimuli

Eleven stimuli were selected from the Viggiano stimulus set (Viggiano, Vannucci, & Righi, 2004) as they were ‘colour diagnostic’ i.e. the objects were associated with a specific colour. To modify the chromaticity of these stimuli the colour of each pixel was rotated by 180° in DKL colour space using custom-written MatLab routines in conjunction with the CRS “Colour Toolbox”. This allowed for systematic manipulation of the colour whilst maintaining luminance and contrast.

All stimuli were rendered on a white background and subtended $2.2^\circ \times 2.2^\circ$ when viewed at the specified distance. These were then presented 8.7° from the left and/or right from a central fixation cross.

Design

Participants were required to verbally report the identity of the stimulus at each location, reporting ‘nothing’ when no item was detected. All eleven stimuli appeared on the contralesional side in each of six conditions both in the original and the inverted colour version. On single-item trials targets were presented in isolation in the contra- or

ipsilesional visual field. The conditions for two-item trials were determined by the identity and colour of the ipsilesional stimulus in relation to the contralesional item. The conditions are detailed below and are illustrated by an example in brackets that assumes that the contralesional stimulus is a correctly coloured green lettuce and specifying the accompanying ipsilesional item.

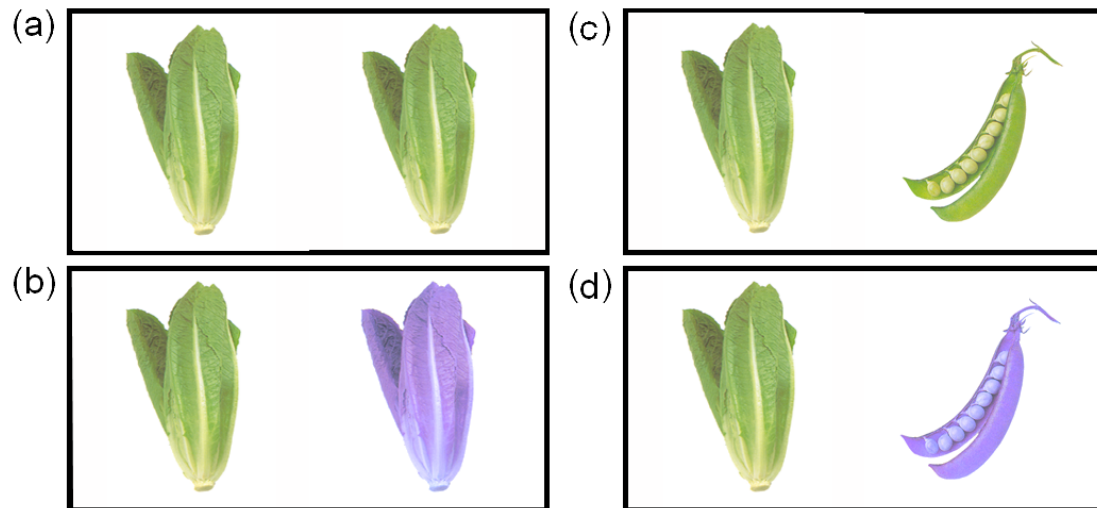


Figure 35: Example stimulus pairings on two-item trials. Here, the contralesional (left) item is a correctly coloured green lettuce depicted in each of the following conditions: (a) *Same Shape, Same Colour*, (b) *Same Shape, Different Colour*, (c) *Different Shape, Same Colour*, (d) *Different Shape, Different Colour*.

Same Shape, Same Colour; Both correct: identical correctly coloured items were presented bilaterally (ipsilesional item: green lettuce, Figure 35a).

Same Shape, Different Colour; Contralesional correct: items differed in colour only such that one item was presented in the original hue and the other in the inverted version (ipsilesional item: purple lettuce, Figure 35b).

Different Shape, Same Colour; Both correct: the items had different identities; both were in the correct, matching colours.

(ipsilesional item: green pea-pod, Figure 35c).

Different Shape, Different Colour; Contralesional correct: items differed both in colour and identity and only the contralesional item was in its correct colour (ipsilesional item: purple pea-pod, Figure 35d).

These four conditions were replicated for when the contralesional item had an incongruent colour (Figure 36).

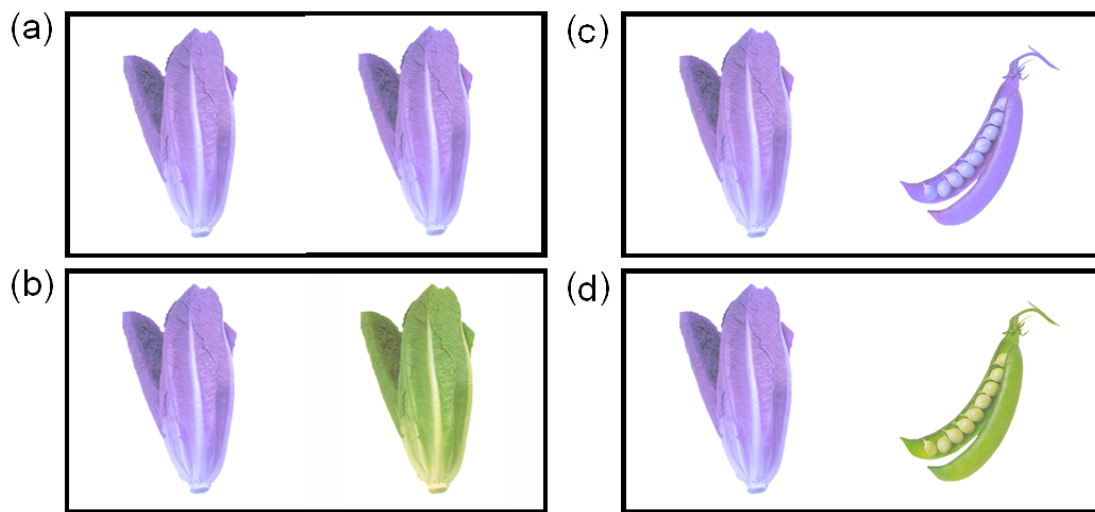


Figure 36: Example stimulus pairings on two-item trials. Here, the contralesional (left) item is a incorrectly coloured purple lettuce depicted in each of the following conditions: (a) *Same Shape, Same Colour*, (b) *Same Shape, Different Colour*, (c) *Different Shape, Same Colour*, (d) *Different Shape, Different Colour*.

Procedure

Prior to testing the experimenter explained the task and each patient was familiarised with the stimuli and the displays. Practice sessions allowed the stimulus duration to be roughly titrated to prevent floor or ceiling effects with approximately 60% accuracy on single item trials. This was done at start of each testing session resulting in different stimulus durations across but not within experimental blocks. The stimulus conditions were randomly presented within each block. The average times per patient are detailed in Table 11.

Table 11: Number of sessions completed, and the stimulus duration used for each patient.

<i>Patient</i>	<i>AS</i>	<i>DB</i>	<i>DT</i>	<i>JW</i>	<i>PM</i>	<i>RH</i>
No. Sessions	5	4	3	4	3	3
Stimulus Duration (ms)	650-750	300-500	375-425	400-450	100-500	550-600

All trials were preceded with a black fixation cross ($0.9^\circ \times 0.9^\circ$) that was presented centrally on a white background. Participants were reminded to maintain fixation on this cross and this was confirmed via experimenter observation. A verbal ‘ready’ warning initiated the start of trial; the fixation was removed and was replaced by the stimulus display. Participants were given unlimited time to make their response, which was communicated orally and written down by the experimenter. For patients who expressed some difficulties with verbal responding (DB, PM, RH) were given an answer sheet that had each item depicted in greyscale and the patients were allowed to point to their selection.

Results

Proportion correct data was converted to arcsin values. This was done because the proportion correct values were quite low, and this transformation moves them towards the centre giving them more freedom to vary. In the analysis each session was included separately and patient was included as a between-subject factor.

The mean proportions of contralesional stimuli correctly identified on one- and two-item trials are displayed in Figure 37. The patients were significantly more accurate at identifying a contralesional item when it was presented in isolation than when it was presented simultaneously with an ipsilesional stimulus (Figure 37, ($F(1, 17) = 35.866, p < 0.001$)), a pattern of performance indicative of visual extinction. There was a slight benefit for correctly rather than incorrectly coloured items but overall this was not overall significant ($F(1, 17) = 2.174, p = 0.159$ n.s.).

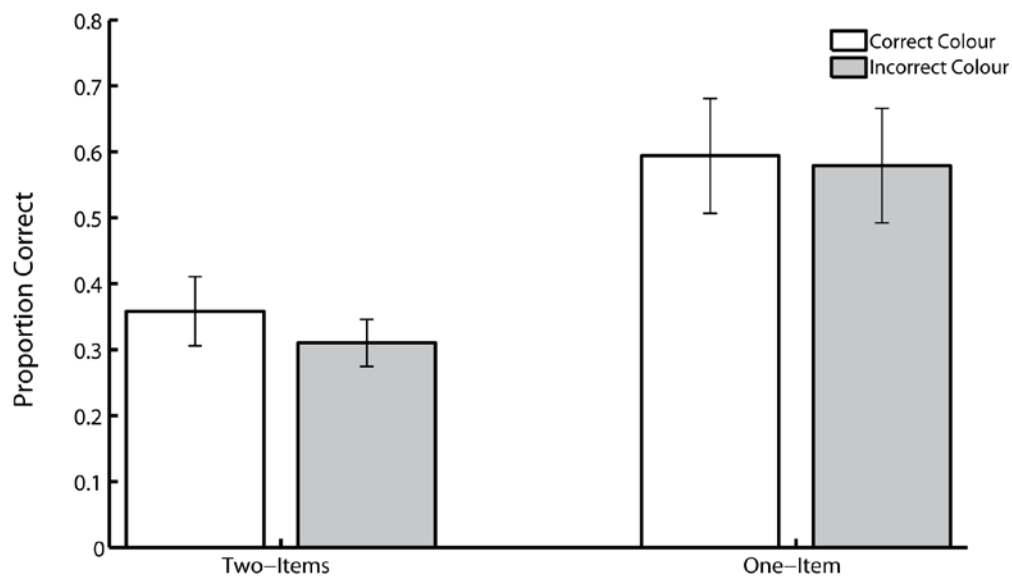


Figure 37: Mean proportion correct reports on one- and two-item trials according to whether the contralesional stimulus was correctly coloured or not. Error-bars represent standard error of the mean.

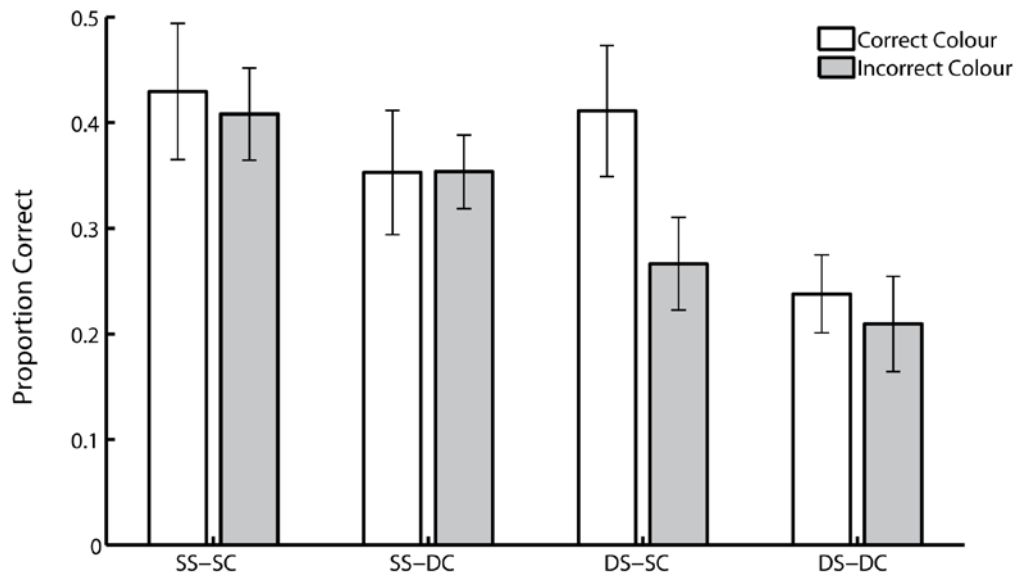


Figure 38: Mean proportion correct in each of the two-item trial conditions. These are: Same Shape-Same Colour (SS-SC), Same Shape-Different Colour (SS-DC), Different Shape-Same Colour (DS-SC), and Different Shape-Different Colour (DS-DC). The colour-shape consistency of the contralesional item is indicated by the bar colour. Error bars indicate the standard error of the mean.

Performance on each type of two-item trial is illustrated in Figure 38. The data were analysed using a repeated measures ANOVA including colour repetition (same / different), shape repetition (same / different), and colour-shape congruency (correct / incorrect) as within-subject factors and patient as between. This analysis returned a significant main effect of both colour repetition ($F(1, 17) = 25.646, p < 0.001$) and shape repetition ($F(1, 17) = 11.313, p = 0.004$) indicating that, for both dimensions, there was a benefit when features were repeated. Overall, inverting the colour of stimuli significantly impaired performance ($F(1, 17) = 7.332, p = 0.015$). Colour-shape congruency significantly interacted with shape repetition ($F(1, 17) = 10.246, p = 0.005$), and a borderline interaction with colour repetition ($F(1, 17) = 3.33, p = 0.086$). Inspection of Figure 5 reveals that these interactions occur because when items shared colour but not shape, performance was significantly better when the items were in their correct colour ($t(22) = 4.113, p < 0.001$). In contrast, colour-congruency has little effect when only the shape is repeated across hemi-field ($t(22) = 0.063, p = 0.95$).

In considering the effects of repetition on extinction, it is important to rule-out the possibility that participants' were biased to make preservative guesses and therefore artificially inflating accuracy on identity repeat trials. These findings however are not consistent with this explanation as the vast majority of errors were due to omissions (91.65% of error trials) rather than incorrect responses. Furthermore, incorrect identification responses did not differ across conditions (see Table 12).

Table 12: Proportion of incorrect trials where patients made an erroneous response (rather than an omission).

	<i>SS-SC</i>	<i>SC-DC</i>	<i>DS-SC</i>	<i>DS-DC</i>
Correct Colour	8.35	8.26	8.53	8.97
Incorrect Colour	9.07	9.32	10.26	13.23

Discussion

The data in Experiment 1 confirm prior studies showing positive effects of stimulus similarity on extinction. Most notably, performance at identifying the contralesional stimulus improved when it had the same shape as the ipsilesional item. This result is consistent with similarity based grouping operating, with the attentional bias against the contralesional stimulus decreasing when this stimulus grouped by shape with the ipsilesional item (Gilchrist, et al., 1996; Humphreys, 1998; Mattingley, Davis, & Driver, 1997; Ward, et al., 1994). The data also indicate some effect of joint sharing of shape and physical colour. Report in condition SS-SC was better than in condition SS-DC, and this held irrespective of whether the stimuli carried their correct colours or not. This suggests that, even though colour was not relevant to report, colour similarity enabled contralesional stimuli to be grouped with ipsilesional items

reducing the extinction effect. The colour effect in this case also interacted with shape similarity since the effect of shared physical colour was ineffective (relative to DS-DC baseline) when the stimuli different in shape and when the items were assigned unfamiliar colours (condition DS-DC, incorrect).

In addition to any effect of shared physical colour, the results showed a substantial effect of stimuli having the correct (known) colour, when items differed in shape (condition DS-SC, correct). In this case, performance was enhanced relative to the all different feature baseline (condition DS-DC). This result suggests that, when the items differed in shape, they could group if they had a common, known colour. Grouping with the ipsilesional items enabled the contralesional item to be recovered and reported. One implication of this argument is that the colour and shape of the contralesional stimuli were bound, even though when stimuli fell in the contralesional field and even though they were otherwise not available for awareness - since otherwise the familiarity of the colour-shape relationship would not have been crucial.

Experiment 2: Testing ipsilesional cueing

I have argued that the results from Experiment 1 reflect grouping between the contra- and ipsilesional stimuli, modulated by the familiarity of the colour-shape relationship (in condition DS-SC). However, an alternative account is possible which proposes that the effects are not due to grouping but rather to the speed of identifying the ipsilesional stimuli. Consider stimuli in condition DS-SC when the colour-form relations were known (red strawberry, red tomato) and when they were unknown (blue strawberry, blue tomato). It is possible that the effect of stimuli having a known colour was because the correctly coloured ipsilesional item could be rapidly identified and this enabled patients to then attend to the contralesional side. Attention might be allocated to the contralesional item then if it matched the colour of the ipsilesional item, so leading to an effect of common colour in the known-colour condition. According to this account, it is the speed of identifying the ipsilesional stimuli (enhanced when they carry a familiar colour), not grouping that is important. This was tested in Experiment 2. In Experiment 2 I included new conditions in which the stimuli had different shapes and the same physical colour, but only the ipsilesional or only the contralesional stimulus had its familiar (correct) colour. According to the ‘ipsilesional identification account’, performance at identifying the contralesional item should be good as long as the ipsilesional item is in the correct colour (e.g. yellow (incorrect) contralesional strawberry paired with yellow (correct) ipsilesional lemon). On the other hand, there should be poor report of the contralesional item if the ipsi- stimulus is in the incorrect colour and the contralesional item is in its correct colour (yellow lemon-yellow strawberry) (in the latter case, the delay in identifying the ipsi-stimulus should slow performance and lead to extinction). For the grouping account though, extinction should be reduced only when the contra-item carries its correct colour and can enter into grouping with a correctly coloured ipsi-item (red strawberry, red tomato).

Method

Participants

Five patients who had suffered a stroke and exhibited visual extinction took part in the experiment (AS, DB, PM, JB and RH).

Stimuli

Twelve 'colour-diagnostic' stimuli were selected from Viggiano stimulus set (Viggiano, et al., 2004). Each item was rendered in their correct (e.g. yellow banana) and an incorrect (e.g. green banana) colour. Incorrect versions were prepared by selecting the correct colour of a different stimulus and using a colour exchange using the colour picker tool provided in GIMP 2.6 image manipulation software. All stimuli were scaled to 222 x 222 pixels and were presented on white equiluminant background.

Design

A 2 (contralesional colour-shape congruency, correct / incorrect) x 2 (ipsilesional colour-shape congruency, correct / incorrect) x 2 (colour repeat / no repeat) design was used. Stimuli were always different shapes. Figure 39 and 40 illustrate two-item trials when the contralesional stimulus was a lettuce. All items appeared in each of the eight experimental conditions. Each stimulus also appeared on a single-item trial where targets were presented in isolation in the contra- or ipsilesional visual field. Each session consisted of 144 trials with the order of conditions and stimuli randomised fully. The number of sessions completed by each participant was determined by their availability and is listed in Table 13.

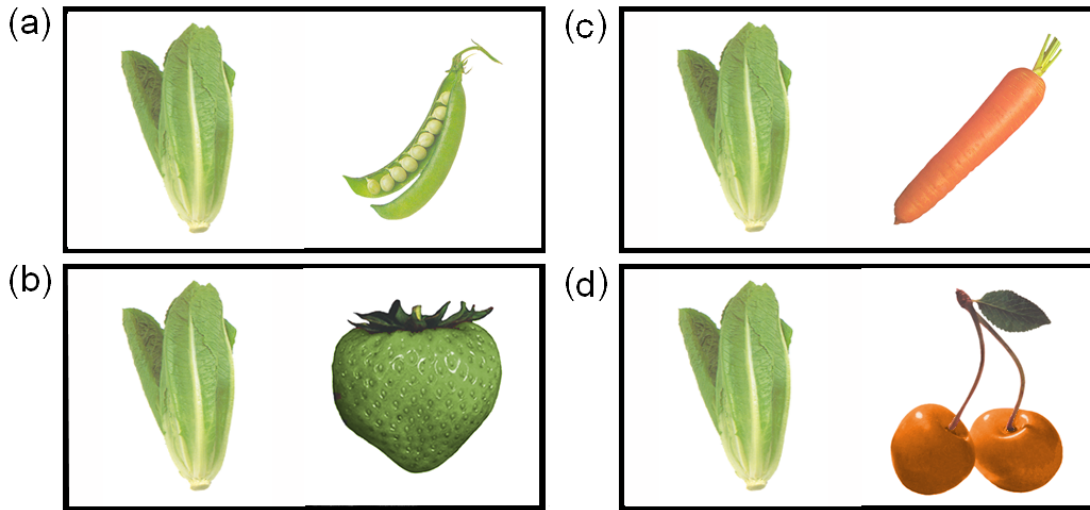


Figure 39: Example stimulus pairings on two-items trials where the contralesional (here left) stimulus is colour congruent (green lettuce). (a) *Same Colour, Both Correct*, (b) *Same Colour, Ipsilesional-Incorrect*, (c), *Different Colour, Both Correct*, (d) *Different Colour, Ipsilesional-Incorrect*.

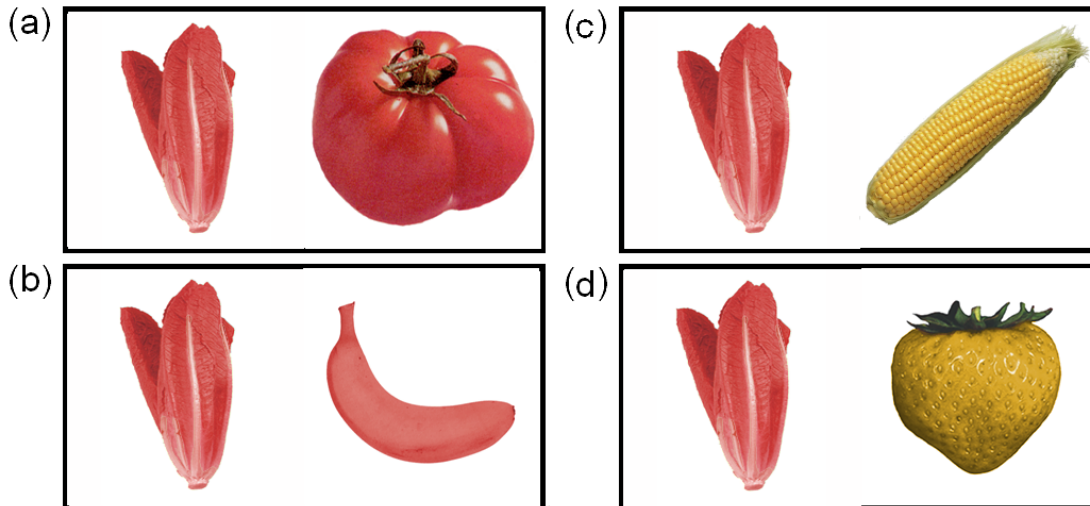


Figure 40: Example stimulus pairings on two-items trials where the contralesional (here left) stimulus is colour incongruent (red lettuce). (a) *Same Colour, Both Correct*, (b) *Same Colour, Ipsilesional-Correct*, (c), *Different Colour, Both Incorrect*, (d) *Different Colour Both Incorrect*.

Table 13: Number of sessions completed, and the stimulus duration used for each patient.

<i>Patient</i>	<i>AS</i>	<i>JB</i>	<i>PM</i>	<i>RH</i>
No. Sessions	3	2	3	4
Stimulus Duration (ms)	600	275	200	500 - 575

Procedure

The procedure was identical to that outlined in Experiment 1.

Results

Again all proportion correct data was converted to arcsin values. In the analysis session was included separately and patient was included as a between-subject factor.

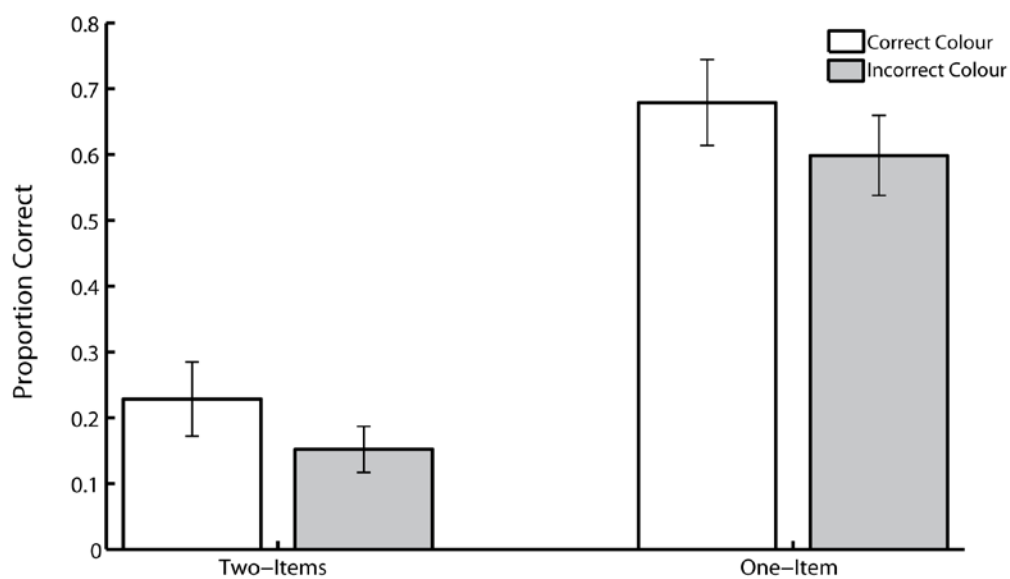


Figure 41: Mean proportion correct on one- and two-item trials according to the colour-shape consistency. Note that when considering two-item trials the colour condition reflects the colour-shape consistency of the contralesional stimulus.

The mean proportions of contralesional stimuli correctly identified on one- and two-item trials are displayed in Figure 41. The data confirmed that patients were significantly more accurate at identifying a contralesional item when it was presented in isolation than when it appeared simultaneously with an ipsilesional stimulus (Figure 41, ($F(1, 10) = 65.486, p < 0.001$)), a pattern of performance indicative of visual extinction. There was a borderline benefit for contralesional items presented in their correct relative to incorrect colour ($F(1, 10) = 4.057, p = 0.072$ n.s.).

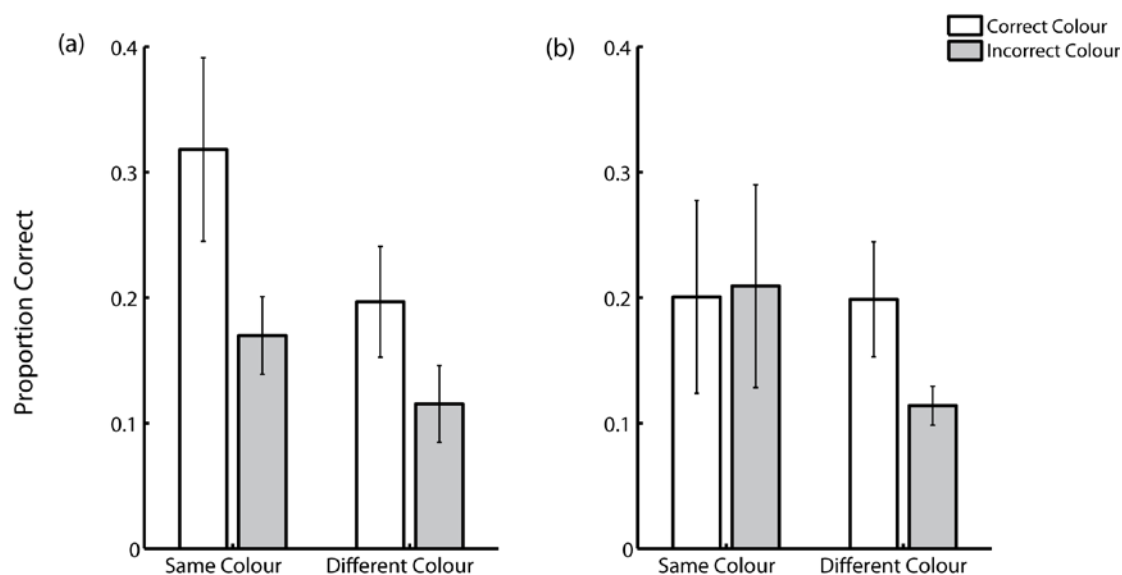


Figure 42: Mean proportion of contralesional items correctly identified when the ipsilesional item was correctly (a) or incorrectly (b) coloured. This is displayed when the colour is the same for both items, and this is the correct (white bars) or incorrect (grey bars) hue for the contralesional stimulus.

Performance in each of the two-item trial types is illustrated in Figure 42. Proportion correct data were analysed using a repeated measures ANOVA including contralesional colour-shape congruency (correct / incorrect), ipsilesional colour-shape congruency (correct / incorrect) and colour repetition (same / different) as factors. This analysis returned a significant main effect of colour repetition ($F(1, 10) = 40.155, p < 0.001$), indicating that there was a beneficial effect of colour grouping. There was also a significant effect benefit of

contralesional item colour-shape congruency ($F(1, 10) = 9.097, p = 0.013$). There was no significant effect of ipsilesional stimulus colour-shape congruency ($F(1, 10) = 1.535, p = 0.244$ n.s.). However, all factors significantly interacted ($F(1, 10) = 5.71, p = 0.038$, for the 3-way interaction). To decompose this interaction, I consider first the trials where the items had different colours. Here there was a main effect of contralesional colour-shape congruency ($F(1, 10) = 13.204, p = 0.005$), but no other effects of interactions. Report was better when the contralesional item was in the correct colour irrespective of whether the ipsilesional item was correctly coloured or not. On trials where the colour was repeated, there was an interaction between the colour congruency of the contralesional and ipsilesional stimuli ($F(1, 10) = 6.459, p = 0.029$). This reflects significantly better performance when both items were correctly coloured relative to when only the contralesional item was correctly coloured ($t(14) = 2.562, p = 0.023$), only the ipsilesional item was correctly coloured ($t(14) = 3.775, p = 0.002$), or neither were correctly coloured ($t(14) = 2.255, p = 0.041$).

Again the majority of errors were due to omissions (90%) rather than incorrect responses, and the incorrect responses did not differ across the conditions (see Table 14). This suggests that the effects were not inflated by participants guessing the contra-target from the ipsilesional item.

Table 14: Proportion of incorrect trials where patients made an erroneous response (rather than an omission).

	Ipsi – Correct Colour		Ipsi – Incorrect Colour	
	<i>Same Colour</i>	<i>Different Colour</i>	<i>Same Colour</i>	<i>Different Colour</i>
Contra-Correct Colour	0.26	0.16	0.16	0.18
Contra-Incorrect Colour	0.15	0.2	0.2	0.12

Discussion

Critically, extinction was reduced most the when the ipsi- and the contra- stimuli were both in the correct colour (and the colour was the same in the two stimuli); it was not sufficient for the ipsilesional item to carry its correct colour and share its physical colour with the contralesional stimulus. These data go against the ‘pure ipsilesional identification’ account of performance, but they accord with a grouping account which assumes that the contralesional stimuli group most strongly when both they and the ipsilesional stimulus has their correct colours; the presence of grouping reduces the likelihood that the contralesional items are omitted.

General Discussion

The findings are consistent with the idea that, despite processing deficits in visual extinction, not only are the basic principles of low-level perceptual organisation spared (Driver, Baylis, & Rafal, 1992; Mattingley, et al., 1997) but there can also be high-level coding of stimulus attributes (e.g., the formation of learned form-colour conjunctions). Here I demonstrate that repetition of shape and colour facilitates contralesional item report, replicating previously reported beneficial effects of inter-item grouping on extinction (Gilchrist, et al., 1996; Pavlovskaya, Sagi, & Soroker, 2000; Pavlovskaya, Sagi, Soroker, & Ring, 1997; Ward, et al., 1994). The beneficial effects of repeated colour occurred here even though colour was irrelevant to the main report task, consistent with the effects of colour and shape similarity arising at early processing stages prior to task-relevance modulating performance. In addition to the effects of shared physical colour, though, I also found learned colour-form relations modulated performance. Notably, when the stimuli had different shapes there was recovery from extinction for items with the same physical and learned colours (red strawberry and red tomato) relative to stimuli with matching physical colours only (blue strawberry and blue tomato). This result did not simply effect the presentation of an ipsilesional item in the correct colour – there was no recovery of extinction when the same ipsilesional item was accompanied by a contralesional item in an incorrect but matching colour (e.g. red lemon and red tomato) (Experiment 2). I conclude that both the ipsi- and contralesional stimuli had to have the same learned colour to enter into strong grouping. This in turn suggests that the shape and colour of contralesional stimuli are bound together pre-attentively, to subsequently form perceptual groups.

How do we interpret these results? One possible explanation for these findings is that top-down object-based representations provide feedback about colour and shape consistency.

There is evidence that processing in the contralesional field can be sufficiently elaborate to extract the identity and semantic details of stimuli even if the items never consciously perceived (McGlinchey-Berroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993; Volpe, Ledoux, & Gazzaniga, 1979). It follows therefore that contralesional stimuli may be processed to a high level allowing congruent associations to be fed-back and to support biases against contralesional stimuli. It seems surprising however that elementary Gestalt grouping process should be modulated by top-down information. An alternative explanation therefore is that learned associations between shape and colour are stored as conjunctive representations. These are activated bottom-up from the image allowing objects to be linked to their familiar colour automatically. In this way congruent colour-shapes are unitised pre-attentively at early stages of processing shaping visual parsing.

These findings have important theoretical implications for theories of both attention and object processing. Firstly, dominant theories of visual processing distinguish between an early pre-attentive processing stage that codes perceptual features in a spatially parallel manner, with binding occurring at a later stage after focal attention (Treisman & Gelade, 1980). However visual extinction patients show (by definition) poor attention to contralesional stimuli yet colour-form bindings appeared to occur. My findings suggest features can be unitised pre-attentively provided the relations between the features are learned. A second issue raised by the findings concerns the role of colour and shape in object processing. Here the findings provide strong evidence for pre-attentive unitisation of combined shape and colour information. It is difficult to reconcile these findings within a purely 'edge-based' account of object processing, which allocate a role for surface information only at a late stage of object identification (Biederman & Ju, 1987). The findings are more parsimonious with a 'surface-plus-edge' account where diagnostic colours could form part of an objects' perceptual representation and are therefore influential at the earliest stage of processing

(Davidoff, 2001; Tanaka, Weiskopf, & Williams, 2001). This is in line with recent evidence from human electrophysiology recordings, that have revealed ERP components indexing early perceptual processing (N1, N2 and P2) differentiate between correctly coloured stimuli and incorrect and gray-scale versions of the same items (Lu, et al., 2010). These findings extend this to indicate that this early mediation of perceptual processing by learned colour-form bindings takes place outside awareness and so become available earlier for grouping. This would fit with the ERP data highlighting the rapid coding of colour-form conjunctions (Lu et al., 2010).

A final point to note here is that I report positive effects of stimulus similarity on visual extinction. In at least some other reports (Baylis et al., 2001; Baylis, Driver and Rafal, 1993), investigators have noted that extinction is increased for similar stimuli. These results are not necessarily contradictory and may depend on several factors, such as the spacing between the items (Riddoch, Rappaport & Humphreys, under review). I used stimuli that were relatively close together and which are likely to group when similar. Under these conditions, clear beneficial effects of similarity arise.

In sum, in a two experiments I find evidence for pre-attentive binding of colour-shape associations, which modulate grouping and recovery from extinction. This indicates that learned colour-shape relations exert an influence at an early stage of processing, guiding selective-attention. These findings have important implications both for theories of visual attention and object processing.

CHAPTER 7

THE NEURAL CORRELATE OF LEARNED BINDINGS

Synopsis

There is considerable evidence that the early stages of visual processing segregate the image into independent features, however our perception is coherent and unified. Here I use fMRI to ask what is the neural ‘site’ of feature binding. Nearly all research addressing this question has used stimuli that have an arbitrary association, which may not be reflective of our environment where many objects have set feature relations. Here I assessed sensitivity to learned feature relation using living items that have an associated, diagnostic colour. Items were depicted in their correct or incorrect hue, with their form scrambled or intact. Intact objects depicted in their correct colour activated regions of the primary visual cortex significantly less than incorrectly coloured versions. This suggests that at the earliest stage of processing the brain is sensitive to the congruency of learned colour-shape associations. These findings suggest that learned conjunctions may be supported by efficient conjunction coding in early visual areas of the brain.

Introduction

There is considerable evidence from neurophysiology, brain imaging and neuropsychology that early stages of visual processing segregate the image into independent features. For example, seminal physiological evidence by Hubel and Livingstone (1987) reported that the visual system was divided into distinct parvo- and magnocellular channels, with, different features of stimuli (their colour, shape, motion) being processed in distinct brain regions. Single cell recordings have demonstrated that within visual cortex there are specialised areas where cells selectively respond to a given feature so that (e.g.) cells in V4 show colour rather than motion selectivity whilst cells in area MT have the opposite stimulus selectivity (Zeki 1973; 1974; 1977). Consistent with this, fMRI studies have shown functional specialisation within the brain with different features are processed in distinct cortical regions (see Kanwisher, 2010), while damage to the distinct regions can generate selective problems in processing particular visual features (e.g., see papers in Humphreys, 1999). Despite this segregation, our perception of the world is coherent and unified. This raises the ‘binding problem’; how does this segregated information become bound? Or more specifically for our concerns, where in the brain does this segregated coding converge? What is the neural ‘site’ of feature binding?

In search of the neural correlates of feature binding, researchers have utilised the visual search paradigm, contrasting activation in (i) conjunction search tasks requiring the binding of features to distinguish the target from distractors, and (ii) feature search tasks where the detection of a specific feature is sufficient. After equating conjunction and feature search for difficulty, Donner et al. (2002) reported higher activation in a region of the IPS in the conjunction task where binding was required. Consistent with this, Wardak, Olivier, Duhamel (2004) reported that deactivation of the lateral intraparietal area in monkeys, the proposed

homologue of human intraparietal sulcus, resulted in impaired conjunction search performance, whilst feature search was unaffected. Matching these physiological data, human neuropsychological cases indicate that damage to posterior parietal cortex disrupts feature binding so that, for example, such patients make abnormal numbers of illusory conjunctions when asked to report the colours and shapes of objects (e.g., see Friedman-Hill et al., 1995; Humphreys et al., 2000; Humphreys, Hodsoll & Riddoch, 2009).

The role of parietal regions in visual binding however remains unclear. Nobre et al. (2003) used similar procedures to Donner et al. (2002) but argued that the proposed 'binding' specific activation can be accounted for by performance efficiency, with posterior parietal cortex recruited to help direct spatial attention (e.g., in difficult feature search as well as conjunction search) but not necessarily for feature binding (selective to conjunctions search). Walsh et al. (1997) further found that administering TMS to the right parietal cortex impaired search when the feature conjunction was novel but not once participants were practiced and the target conjunction learned. They suggest that parietal cortex is involved in binding novel but not learned feature conjunctions. Using fMRI, Frank et al. (2011) similarly reported a decrease in parietal activation once the conjunction was established. In addition they present a novel finding that this parietal decrease was accompanied by a corresponding increase of activation in early visual areas. This suggests that learned feature binding may be coded in early visual areas, independently from attention association parietal regions.

There is other evidence implicating early visual areas in binding learned conjunctions. Lu et al. (2010) collected human electrophysiology recordings whilst participants viewed stimuli that have a 'diagnostic colour' i.e. whose shape and colour are consistently associated. This revealed that ERP components indexing early perceptual processing (N1, N2 and P2) differentiated between correctly coloured stimuli and incorrect and gray-scale versions of the

same items. This is consistent with an fMRI study by Zeki and Marini (1998) who compared participants' BOLD response during passive viewing of natural objects presented in correct colour, incorrect colour and achromatic depictions. They reported differential brain activation in the three display conditions. Unfortunately colour conditions varied not only chromatically but also in luminance and contrast necessitating a cautious interpretation of their results. Nonetheless, contrasting activations during viewing of appropriately and inappropriately coloured objects resulted in differences in V4, the fusiform gyrus, hippocampus and ventrolateral portion of the frontal cortex. Edwards et al. (2003) reported that cells in the macaque superior temporal sulcus and inferior temporal were affected by the presence of colour. Strong responses were recorded during the presentation of correctly coloured images but this was greatly reduced when achromatic depictions were observed, and this was suppressed further when stimuli were incorrectly coloured. These differences were seen in the earliest responses (~91ms), again suggesting that for learned associations, colour-shape congruency is extracted rapidly.

A series of studies by Cant et al. (2007; 2009) and Cavina-Pratesi et al (2010) have used fMRI to examine brain regions selective for independent features (e.g., shape and colour) as well as 'common regions' that respond to all features. Multi-feature areas were reported in the fusiform gyrus including the putative 'face' and 'scene' area, suggesting that processing of complex stimuli may include multiple feature types. These studies however used geometric stimuli that have no learned association with their surface features. These areas therefore may respond to multiple-features but may not be sensitive to the appropriateness of their binding.

In the current study I use fMRI to examine visual and temporal regions that are sensitive to the appropriateness of feature binding. The experiment is similar in design to that initially reported by Zeki and Marini (1998) but includes some critical modifications to extend as well

as replicate their initial findings. Firstly, I use a large stimulus set of fruit and vegetables that have a ‘diagnostic’ colour. The stimuli are presented as single items on a plain background, rather than within a scene. This difference is important because there is increasing evidence implicating colour in scene processing, and this could be due to its role in segregating and organising information (Oliva and Schyns, 2000), rather than feature-binding. Secondly, I include a scrambled version of correctly and incorrectly coloured stimuli in order to separate regions that are responsive to different colours rather than those that depended on their conjunction with shape. This is important because inverted colours are typically unusual in our environment and this may confound any effects. Finally, I asked participants to engage in an object one-back task, rather than passive viewing in an attempt to equate the attention demanded by the different stimuli.

Method

Participants

Eleven right-handed and neurologically healthy students at the University of Birmingham (age range: 18-30, mean age: 24, 6 males) gave their written informed consent to participate in the study. All observers reported normal / corrected acuity and normal colour vision.

Stimuli

The stimuli used were 74 colour images of natural objects (180 x 180 pixels) taken from the Viggiano stimulus set (Viggiano, Vannucci, & Righi, 2004) and the authors' own collection. Stimuli were prepared on a square aperture on an equal-luminance white background.

Incorrectly coloured versions of each stimulus were generated by rotating the colour of each pixel by 180° in DKL colour space using custom-written MatLab routines in conjunction with the CRS "Colour Toolbox". This allowed for systematic manipulation of the chromaticity whilst maintaining luminance and contrast.

Eight participants rated the stimuli for diagnosticity (1 - the colour of the object is atypical to 5 - the colour of the object is typical). Consistently high ratings were given for correctly coloured items and low rating for incorrect depictions, confirming that our assignment of correct and incorrect colours was appropriate (a full list of stimuli can be found in Appendix 3).

Scrambled versions of correctly and incorrectly coloured stimuli were generated in accordance with previous studies (Kourtzi and Kanwisher 2000) by dividing the intact images on a 12 x 12 grid and scrambling the resulting squares in three rings to roughly preserve

image density. The black grid was rendered on both scrambled and intact versions (see Figure 43 for an example) Importantly this condition allowed us to disambiguate response differences between correct and incorrect colour conditions due to shape-colour associations and low-level information (e.g. overall colour content).

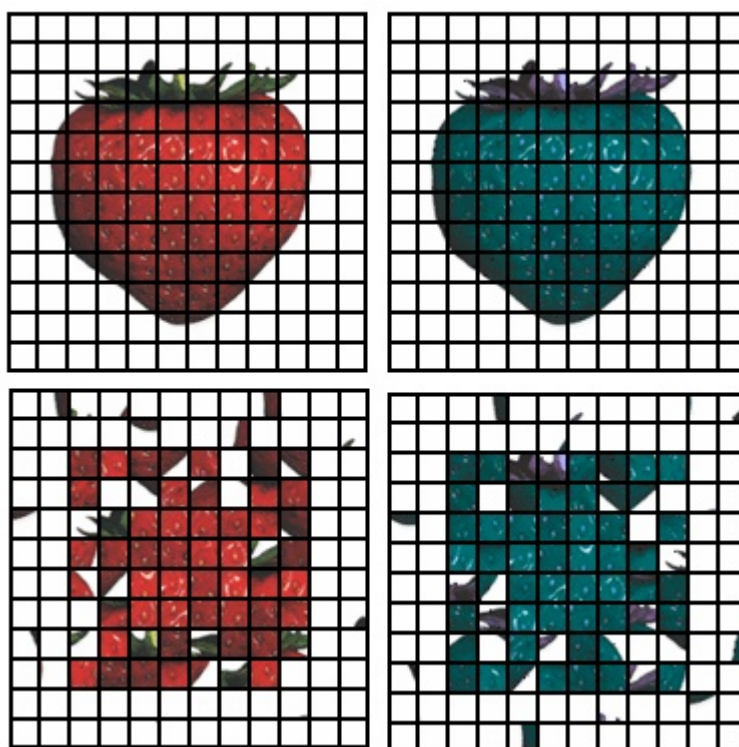


Figure 43: Example of one strawberry stimulus illustrated in its correct (left of figure sub-part) and incorrect (right of figure sub-part) colours. The lower part of the figure the items are scrambled.

Design and Procedure

A 2 x 2 experimental design was employed that manipulated the colour of stimuli (correct / incorrect) and its form (intact / scrambled). Each condition block was presented for 18 seconds, which contained 18 stimulus presentations. Each of the seventy-four exemplar stimuli was repeated four times per run, once in each experimental condition but never within a condition. Each run comprised of four counter-balanced blocks (organised according to a Latin square) of each of the four experimental conditions and blocks of fixation (1 at the start,

1 at the end, and 3 between every set of 4 experimental blocks) and took 5.6 minutes to complete (amounting to 169 volumes). Participants completed four/five sessions of the experimental task.

Each trial began with a black fixation cross presented centrally on a white display for 500ms. The fixation cross was offset and stimuli were presented centrally for 500ms and proceeded by 500ms of a blank inter-trial-interval. Observers completed a one-back repetition task responding with a key-press when two items in direct succession were identical. Such repetition target trials were presented twice per block roughly once in first half of displays and once in the second half; this ensured participant's were attending to the stimuli throughout. Stimuli were back-projected onto a screen that the participant viewed through a mirror-system mounted on the RF-head coil.

MRI data acquisition

Data were acquired in one imaging session at the University of Birmingham's BUIC imaging centre using a 3T Philips Achieva MRI scanner with an eight channel phase array coil. Anatomical images were acquired with a T1-weighted sequence (1mm x 1mm x 1mm). Functional data were blood oxygenated level dependent (BOLD) weighted acquired using a single shot echo planar imaging (EPI) sequence. Thirty-two slices were collected (TR = 2 sec; voxel dimensions, 2mm isotropic, TE = 35ms), positioned with the emphasis on covering early visual areas and the entire temporal lobe.

fMRI data analysis

Pre-processing and statistical analysis of MRI data was performed using SPM8 (Wellcome Department of Imaging Neuroscience; <http://www.fil.ion.ucl.ac.uk/spm>) on a MatLab platform. For each subject the first five volumes were discarded to allow for equilibrium

effects. The remaining functional data were motion corrected, and low frequency drifts were removed using a high-pass filter. The functional data were co-registered to the subject's own anatomical scan and transformed into standard MNI co-ordinates (Montreal Neurological Institute). Lastly the data were smoothed (8mm^3 Gaussian kernel). Statistical analysis proceeded in two steps. Firstly, we used a within-subject univariate general linear model (GLM, Friston, 1994). For each subject a model was created defining the onsets of the four experimental conditions, convolved with the canonical hemodynamic response function (Friston et al., 1998). This also included nuisance covariates of a high pass filter (1/128 Hz) to model low fluctuations and six realignment parameters to account for motion artefacts. To test for consistency across observers, I used a random-effect analysis at the group level.

Results

Behavioural

Participants performed the one-back task with ease (mean accuracy: 80%, mean response time: 451ms). A repeated measures ANOVA analysis of accuracy and response time including form (intact / scrambled) and colour (correct / incorrect) returned no significant effects indicating that performance was equivalent across conditions.

NeuroImaging Results

I focus on results that survive family wise correction at the cluster level, with voxels showing $Z > 2.42$.

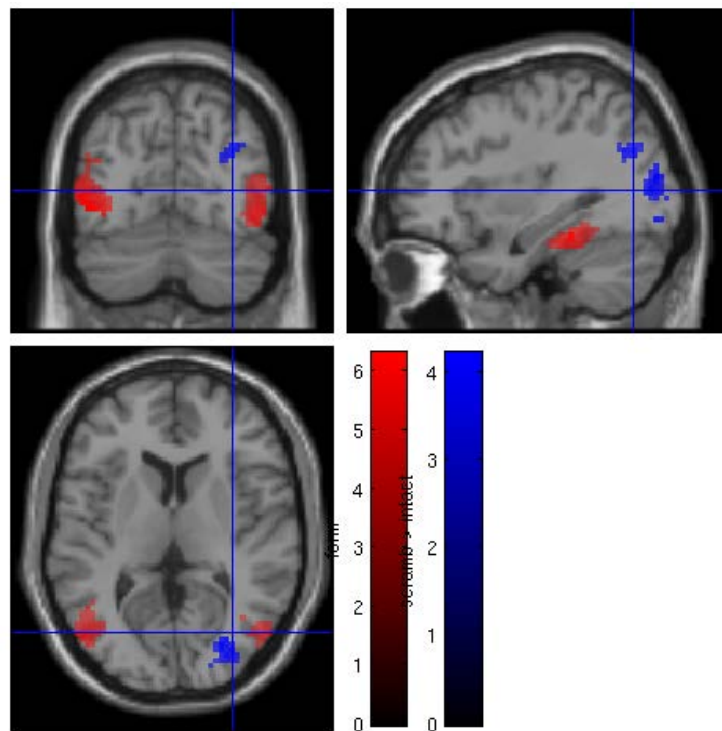


Figure 44: Marked in red are those regions that are significantly more activated by intact relative to scrambled items, and in blue those regions showing the reverse of this contrast.

Firstly I considered the effect of item form by contrasting activations to intact and scrambled depictions of our stimuli, averaged across the two colour conditions. I found two regions in the temporal lobe that showed significantly greater activation to intact relative to scrambled pictures of items (Figure 44, Table 15). This activation was seen bilaterally and included a cluster spanning the middle and inferior occipital gyrus, extending to the inferior temporal gyrus and fusiform gyrus. This corresponds with the putative object-selective LOC (Kourtzi et al., 2003). The reverse contrast (i.e. regions that show significantly more activation when items are scrambled rather than intact) included regions of the right middle occipital gyrus (Figure 44, Table 15).

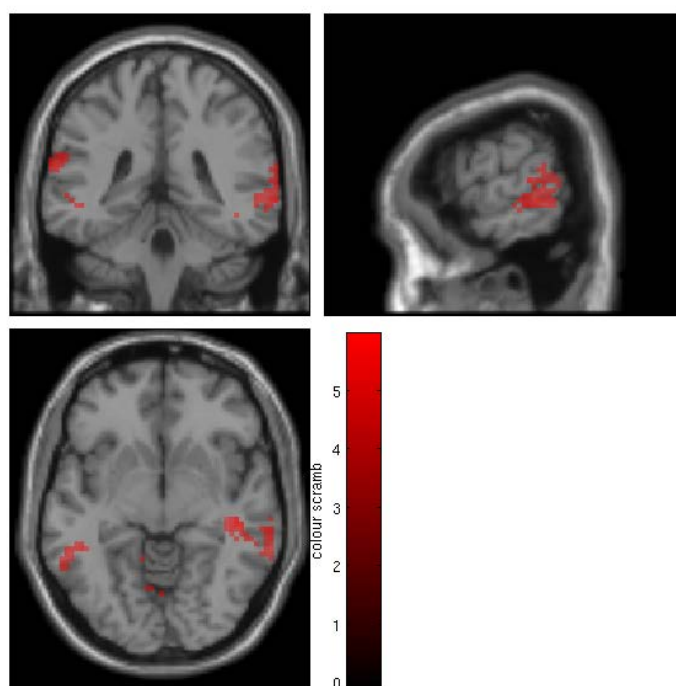


Figure 45: Regions that show significantly more activation to scrambled items that are correctly relative to incorrectly coloured.

Next I considered whether there are areas sensitive to different colours irrespective of the item's form. Contrasts taken across correctly and incorrectly coloured depictions failed to reveal any significant differences. Taking only the scrambled condition, there was

significantly greater activation for stimuli carrying the correct relative to the incorrect colours in bilateral middle and inferior parts of the temporal gyrus, the superior temporal gyrus and the fusiform gyrus (Figure 45). This cluster did not overlap with any other reported regions. The greater activation for correct over incorrect colours might reflect the differential frequency of these colours in the environment.

Table 15: Cluster significant at whole brain corrected for multiple comparisons at 0.05 level

<i>Region</i>	<i>T</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>Cluster Size</i>
Form Intact > Form Scrambled					
Left occipital, temporal and fusiform gyrus	6.30	-48	-70	-1	634
		-45	-52	-17	
		-30	-43	-20	
Right temporal and fusiform gyrus	6.21	42	-34	-5	402
		51	-67	-5	
		45	-67	-11	
Form Scrambled > Form Intact					
Right middle occipital gyrus	4.20	30	-88	16	189
		27	-79	7	
		30	-70	25	
Scrambled Correctly Coloured > Scrambled Incorrectly Coloured					
Left temporal and fusiform gyrus	5.01	-63	-49	-2	180
		-69	-37	19	
		-48	-43	-8	
Right temporal and fusiform gyrus	4.09	69	-43	-5	227
		45	-22	-20	
		48	-31	-17	
Intact Incorrectly Coloured > Intact Correctly Coloured					
Right lingual and calcarine gyrus	3.11	15	-76	-17	112
		18	-79	-5	

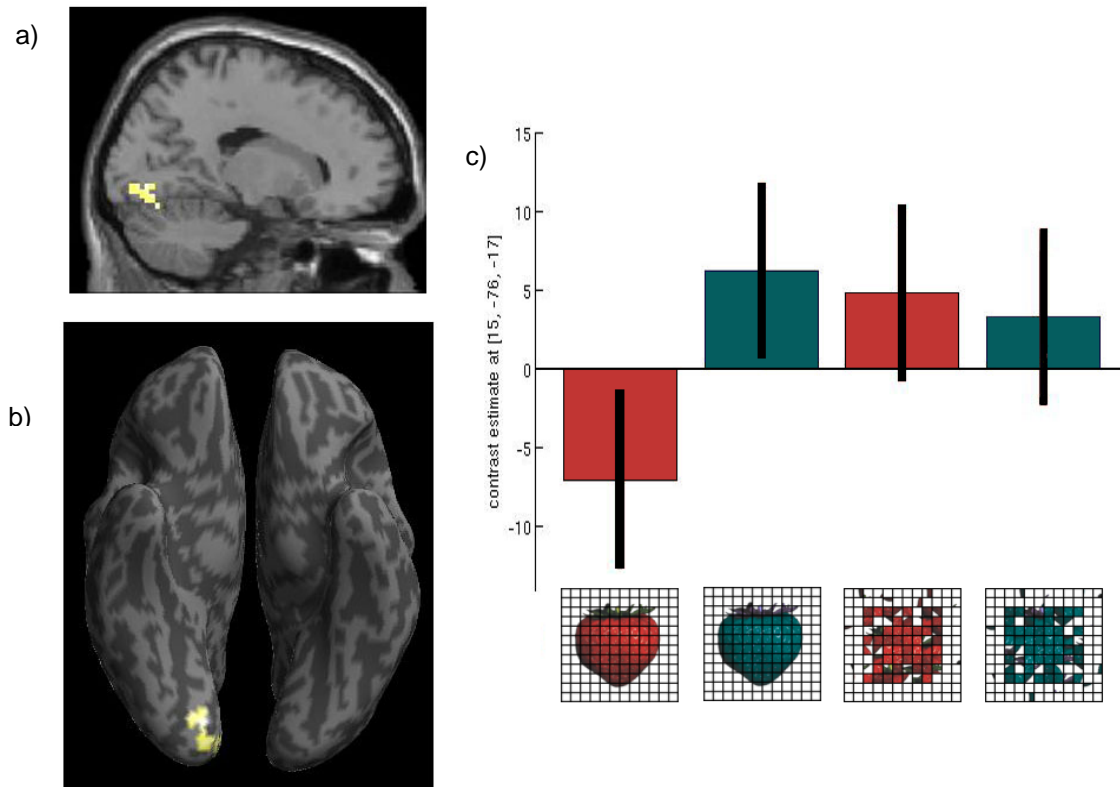


Figure 46: Intact items incorrectly > correctly coloured: (a) Overlaid on a sagittal view of the MNI canonical brain with the right hemisphere in view. (b) Rendered on an inflated brain mesh, showing the inferior view. (c) Bar graph showing the effect size (BOLD signal change relative to the global brain mean) at the site of peak activation within this cluster for all four experimental condition. Error-bars indicate 90% confidence intervals.

The main aim of this study, however, was to examine whether there are regions that show sensitivity to the congruency of learned colour-shape bindings. To test this, I compared activation when intact items were correctly vs. incorrectly coloured. This contrast revealed a significant difference in early visual cortex, including the lingual and calcarine gyrus (likely corresponding to primary (BA17) and extrastriate (BA18) visual cortex (Table 15, Figure 46)). Specifically in these regions there was significantly less activation when the intact item was depicted in its correct relative to incorrect colour. Critically, activation within this cluster does not differentiate between scrambled versions of correctly and incorrectly coloured items. This indicates that regions of early visual cortex are sensitive to the presence of familiar colour-shape conjunctions.

Discussion

In the present study I demonstrate that early visual regions are sensitive to the congruency of colour-shape binding. Objects depicted in their correct colour activated regions of the primary visual cortex significantly less than incorrectly coloured versions. This suggests that, when features have a learned association, the appropriateness of their pairing affects processing at the earliest stage. In addition, it suggests that processing consistent bindings is computationally less costly and more efficient than processing inappropriate pairings.

These findings are consistent with the notion that, through learning, the brain may establish ‘hard-wired’ conjunctive representations (VanRullen, 2009). These may be accessed bottom-up from the image at the earliest stage of processing and do not engage costly attention mechanisms. Consistent with this, Rappaport, Humphreys and Riddoch (*in press*, Chapter 5) showed that there was pop-out for learned conjunction-like targets but not when the same items carried incorrect colours (for yellow but not purple corn), and this occurred even when the correctly coloured target was a low probability event. The present results identify the neural correlate of this ‘pop-out’ for familiar targets whose features have a learned association. In contrast, stimuli with arbitrary feature relations, as used in the vast majority of visual search experiments, may require an ‘on-line’ system mediated by attention. This distinction is supported by a growing number of studies implicating parietal association regions in conjunction search when the relation between features is meaningless, but early visual areas once the conjunction of features is established (Walsh et al., 1997; Frank et al., 2011). An alternative account of the present results is that the decreased activity in early visual cortex may result from feedback from parietal regions to visual cortex (see Treisman, 2006). However this is not easily reconciled with electrophysiological evidence showing

rapid neural responses distinguishing between objects in their correct and incorrect colour (Lu et al., 2010).

These findings have important implications for theories of object processing, where the role of colour is at the heart of the distinction between ‘edge-based’ and ‘surface-plus-edge’ theories (e.g., Biederman & Ju, 1987; Price & Humphreys, 1989). ‘Edge-based’ theories allocate a role for colour (and other surface information) only at a late stage of processing once edges have been resolved. The findings that early visual areas are sensitive to the binding of colour and shape are not easily reconciled with a pure edge framework; rather they support a ‘surface-plus-edge’ account where diagnostic colour is an integral part of object processing (Price & Humphreys, 1989).

In conclusion, I examined the binding problem by considering how learned colour-form associations are coded in the brain. I find evidence of efficient coding of learned conjunctions in early visual areas consistent with automatic and pre-attentive unitisation of features when they have a learned association. My findings emphasise that learning perceptual binding allow us to overcome attentional limitations when processing multi-feature objects, which may be critical for efficient perception in complex, real-world environments. By learning feature bindings, the brain may also establish a type of predictive coding in early vision for statistical regularities in the environment.

CHAPTER 8

GENERAL DISCUSSION

This thesis was motivated by the ‘binding problem’; how segregated information is unified and our perception made coherent and whole. In the presented work I examined two ways in which the brain may overcome the binding problem. Part 1 described two neuropsychological studies examining the effects pre-attentive grouping on extinction. Part 2 examined the effects of learned associations on feature binding. Although both parts consider binding of visual information, integration across the visual field might involve different processes to binding features of an object. This section therefore is separated into these two themes and will finish with some general conclusions.

Part 1: The effects of item similarity on extinction; when and how is it beneficial?

The overall aim of the first section of this thesis was to examine the effects of grouping on the extinction deficit. I considered how procedural differences may be important in modulating the effects of item similarity, and whether beneficial effects of similarity can be understood within a framework in which patients have temporal and spatial processing impairments.

Overview of the findings

The aim of Chapter 2 was to re-examine the effects of item similarity on extinction. Within the literature seemingly discrepant results of both beneficial and detrimental effects item similarity on the extinction deficit have been reported (Baylis et al., 1993; Gilchrist et al., 1996; Humphreys, 1998; Pavlovskaya et al., 2000; Ward et al., 1994). My aim was to

understand how and when these discrepancies arise. Two key procedural differences present across previous experiments were systematically manipulated: i) element inter-item distance and ii) the presence of a central fixation cross. In a series of four neuropsychological experiments I demonstrated that performance could be shifted from negative to positive effects of stimulus similarity on extinction. Item similarity reduced extinction under display conditions that promoted perceptual grouping (with small separations between stimuli, with the fixation cross removed when the targets onset). In contrast, both item repetition and the repetition of task-relevant features exacerbated extinction under display conditions that discouraged grouping (with wide separations and with the fixation cross maintained throughout the trial).

Chapter 3 further examined the effects of grouping on extinction considering for the first time whether grouping modulates the temporal as well as the spatial coding of stimuli. In a temporal order judgment task, patients with visual extinction had a bias against the contralesional item appearing first. This bias however was reduced when items grouped by shape and colour.

Theoretical Implications

Beneficial effects of grouping, and detrimental effects of task-relevant repetition, have been previously replicated and are reported again here in this thesis. Both findings must be taken into account in a theory of visual extinction. To explain the results I suggest that extinction may arise at at least two distinct stages of processing. ‘Extinction’ may not be a single phenomenon.

1) Parsing

Extinction patients may show impairments on initially registering a contralesional stimulus at an early processing stage, which is positively modulated by perceptual grouping. Perceptual grouping may ‘yoke’ the contralesional stimulus to a strong representation of the ipsilesional item, altering the spatial and temporal coding of the contralesional item and positively modulating initial parsing. As reported in Chapter 2 and 3, under display conditions that promote perceptual integration, extinction is less severe: there are reduced omission errors and reduced temporal order biases.

These findings have implications for our understanding of normal early visual processing. By definition visual extinction patients show poor attention to contralesional stimuli, yet visual low-level perceptual organisation seemed to occur (otherwise it could not modulate extinction). This evidence adds to the growing consensus that initial visual parsing occurs pre-attentively, organising information for subsequent attentive processing (Kimchi & Razpurker-Apfeld, 2004; Lamy, Segal, & Ruderman, 2006; Moore & Egeth, 1997). Consistent with this, perceptual grouping was not necessarily modulated by the task-relevance of the feature repetition. Rather, beneficial effects of grouping were seen predominantly when both items were identical. I reason therefore that low-level pre-attentive processes that are sensitive to the display structure, rather than task-relevance, drive positive effects of grouping on extinction.

2) Encoding into VSTM

I propose that extinction patients are not only impaired at early perceptual parsing but also at a later stage of encoding items into visual short-term memory, which is negatively modulated by stimulus similarity. This aspect of the extinction deficit could be understood as a ‘repetition blindness’ effect when generating ‘tokens’ of the same ‘type’ as detailed by Baylis et al. (1993, and developed into a dorsal-ventral disconnection in 2001). Within this

framework for an object to be encoded ‘type’ (or feature, coded in the ventral stream) and ‘token’ (or location, coded in the dorsal stream) information must be bound. In visual extinction, damage to the parietal lobe disrupts dorsal stream processing resulting in compromised ‘token’ (location) information for successfully processed ‘types’ (features). Couched in these terms visual extinction patients detect a single contralesional item because there is normal ‘type’ information that must be accounted for, and so the degraded location information is requisitioned. The encoding difficulty however is exacerbated when ‘types’ are not sufficiently unique. In this case the ‘type’ can be explained by the ipsilesional location information alone, never requiring the degraded contralesional ‘token’. Since perception requires encoding of bound types and tokens a contralesional item sharing a task-relevant dimension may be omitted.

Directions for future research

fMRI

One direction for future research would be to examine the neural substrate of beneficial grouping on extinction, particularly because there are clear predictions from healthy participants. If this alleviation were as I suggest due to early grouping processes, one would expect it to be associated with neuronal activity in early regions of the occipital and temporal cortices. Using fMRI it would be interesting to examine activation when items group vs. do not group. Rees et al. (2000) have shown that patients that have suffered parietal damage show reduced activation in early visual regions. When items group and the contralesional stimulus recovered is there still this reduction? This might be important in addressing the question of whether grouping in extinction operates ‘normally’. I have clearly shown that contralesional items can enter into grouping, but this does not mean that these processes operate normally. If, and how, they may differ are pertinent questions for future research.

Part 2: Binding of learned features

The overall aim of the second section of this thesis was to examine the binding of colour and shape when they have a learned relationship i.e. when colour is diagnostic for the object. Using a variety of methods I provide converging evidence that the brain may store the conjunction of features associated with known objects. I review the main findings of each chapter in turn and consider how they contribute to this conclusion.

Overview of the findings

The aim of Chapter 4 was to examine the effects of surface colour on object processing. It was hypothesised that associated colour and shape are automatically integrated in an object's representation. To test this hypothesis I examined whether congruent colour-shape associations can interfere with as well as facilitate with processing. The novelty in this experiment comes from measuring interference as an index of automaticity, where previously only facilitation of colour-shape congruency has been studied (Price & Humphreys, 1989; Tanaka & Presnell, 1999; Wurm et al., 1993; Naor-Raz, Tarr, & Kersten, 2003). The results show that colour –shape congruency can interfere with object naming. Under short exposures (Chapter 4, Experiment 2) interference of congruent colour on colour-naming was observed. For example, participants named strawberry more efficiently if it was depicted in blue (incongruent) compared with red (congruent). These effects were observed only when the colour depicted the objects surface, not when it fell in the surround. I reason therefore this interference reflects access to perceptual representations of objects that code surface colour as well as form. With long exposures (Chapter 4, Experiment 1) inference of congruent colour was observed both when the hue depicted the items surface or surround, suggesting that there can also be interference from the joint activation of object identity and colour properties in semantic memory.

Chapter 5 further explored automatic colour-shape integration by asking whether this binding occurs without selective attention. I presented a series of difficult visual conjunction-search experiments, of similar targets and non-targets, using objects that have an associated colour. I reasoned that for incongruent associations this difficult search would require serial processing and yield a steep search function, whereas pre-attentive binding of congruent colour-shape would be evidenced by shallow parallel search functions. This search pattern was confirmed in Experiment 1a, where yellow corns ‘popped-out’ whereas orange and purple corns did not. Replacing objects with geometric shapes in Experiment 1b confirmed that the advantage for yellow corns was not due to an intrinsic saliency of the hue yellow but rather the congruency of the colour-shape association. In Experiment 1c stimuli were converted to greyscale and the colour previously depicting the items surface now filled its surround. Congruency of the colour surround had no effect on search confirming that the advantage for yellow corn was not due to participants predicting the target colour from the distracters (since the relation between the colours of the distracters and the target held when the hue fell in the surround). Also consistent with Chapter 4, simply the presence of a congruent colour is not sufficient, rather these effects depend on colour-form integration. Experiment 2 questioned whether the efficiency of search for a learned colour-form conjunction target was due to participants’ employing a strategy based on an expectancy of correct colour-shape associations. To address this I biased target type frequency favouring incorrectly coloured targets and examined eye-movements. Although eye movements confirmed an expectancy bias consistent with target frequency, search slopes were still shallower for infrequent correctly coloured yellow corns. In Experiment 2 I extended these findings using a different stimulus set and orthogonally manipulated target and non-target colour-shape congruency (i.e. presenting a correctly coloured target amid incorrectly coloured non-targets, and vice-versa). Overall here I provide

evidence for automatic binding of congruent colour-shape, which manifests as ‘pop-out’ targets and faster rejection of non-targets.

In Chapter 6 I reported two neuropsychological studies to test my hypothesis that colour-shape binding occurs pre-attentively. A critical test of pre-attentive processing comes from studying visual extinction patients. These patients’ pre-attentive processing continue to operate whilst their later attentive processing does not. In Experiment 1 I report that the extinction deficit was less severe when items grouped based on shared i) shape and ii) colour. Critically colour-shape congruency modulated performance. Extinction was less severe when items share both a common physical and known colour (e.g. red strawberry and red tomato) relative to when they only share a common physical colour (e.g. blue strawberry and blue tomato). Experiment 2 confirmed that this could not be attributed simply to the correct colouring of the ipsilesional item. These findings replicate those previously showing a benefit of inter-item grouping on extinction; uniting items pre-attentively allows both to be selected. Importantly this grouping effect is particularly strong when items share the same ‘correct’ colour. I reason therefore that congruent colour and shape binding occurs pre-attentively, to subsequently form perceptual groups.

In the final Chapter I used fMRI to consider the neuronal correlates that may support pre-attentive colour-shape binding reported here. Items were depicted in their correct or incorrect hue, with their form scrambled or intact. Intact objects depicted in their correct colour activated regions of the primary visual cortex significantly less than incorrectly coloured versions. This suggests that, at the earliest stage of processing in the cortex, stimulus coding is sensitive to the congruency of colour-shape associations. These findings suggest that automatic and pre-attentive unitisation of learned conjunctions reported in my behavioural

experiments may be supported by efficient conjunction coding in early visual areas of the brain.

Taken together these findings suggest that when features have a learned association the visual system avoids the processing limitations apparent for binding arbitrary shapes and colours (Treisman, 1998; Treisman & Gormican, 1988; Treisman & Gelade, 1980). Rather related features are bound early without engaging major attentional limits (Chapter 4), without engaging spatial attention (Chapter 5, 6) and the binding of these features is supported by early visual areas of the brain (Chapter 7).

Theoretical Implications

Feature Integration Theory

A fundamental tenant of FIT is that processing capacity is limited and attention is required for binding object features. The findings presented in Part 2 of this thesis appear contrary to this claim since (i) attentional limitations differed for stimuli with learned vs. those with novel colour-shape relations (Chapter 5), and (ii) binding of learned features appeared to operate pre-attentively, modulating extinction in neuropsychological patients (Chapter 6). It is however important to consider whether there is any room for these results within the FIT.

Evidence demonstrating that, in natural scenes, processing may advance to a high level without being strongly limited by attention is not new (Potter, 1975, 1976; Li et al. 2002; Van Rullen and Thorpe, 2002). For example, Li et al. (2002) reported that participants were able to successfully discriminate briefly presented peripheral animals or vehicles despite their attending to a central, and demanding, letter discrimination task. Advocates of FIT have challenged whether conjunction-coding is really required for such category discriminations

however. Evans and Treisman (2005) for example demonstrated that in the context of sub-optimal attention, participants were able to detect an animal but not identify or localise it. They argued that such processing could be supported by ‘multiple parallel feature detection’ of unbound elements. Detection of a bird in a cluttered scene therefore does not necessarily require spatial attention; rather the bird can be discriminated by its unique “elementary” beak feature. This mechanism however cannot account for the findings in Chapter 5. In all display conditions the same shapes and colours were presented and I varied only the appropriateness of their combinations. ‘Pop-out’ search was only seen when the objects were depicted in their correct colour whereas incorrect combinations of the same features were inefficiently detected. This evidence is difficult to reconcile with the idea of unique feature detection as familiar targets were defined only by their unique conjunction of features.

Within the FIT account it also seems difficult to argue that the evidence of early colour-shape binding results from feedback from parietal regions to visual cortex (see Treisman, 2006). For example, the patients reported in Chapter 6 typically had posterior parietal lesions, while there was no evidence for parietal activation to learned feature bindings in the fMRI data (Chapter 7). It is also the case that electrophysiological evidence shows rapid neural responses distinguishing between objects in their correct and incorrect colours (Lu et al., 2010). I conclude that the data do not mesh with FIT, suggesting that some other account of learned bindings is required.

Temporal Synchrony

The findings can be incorporated into the temporal correlation account, whereby synchronicity of neural firing is proposed to index that features belong together (Singer & Gray, 1995). Synchronous activation of low-level feature neurons may result in a unique cell assembly that defines the object. Repeated encounters with a stimulus may strengthen the

connections between units in the defining assembly (Hebb, 1949). Familiar objects thus come to benefit from a well-defined but distributed neural code, whereas responses to features of unfamiliar conjunctions are not strongly interconnected and may rely on other processes (e.g., slow-acting feedback from parietal to occipital cortex; Braet & Humphreys, 2006). Importantly, the coding of conjunction of features is not inherently rate limited, and maybe more or less efficient depending on the strength and uniqueness of the neural assembly.

Alternative accounts of binding

A further view is that, through learning, the brain establishes learned conjunction representations (rather than assemblies of feature units) (VanRullen, 2009). These individual conjunctive representations are activated bottom-up from the image and act to guide attention to the locations of the ‘trigger’ stimulus. There is emerging neurophysiological evidence for the existence of conjunctive representations from early cortical regions through to infero-temporal cortex (Rust & DiCarlo, 2010; Seymour et al., 2009, 2010, Chapter 7 here), along with electrophysiological evidence from humans for a rapid neural response to objects appearing in the correct colour (Lu et al., 2010), and these conjunctive representations may provide the neural substrate for the present effects. On the other hand stimuli with arbitrary feature relations, as used in the vast majority of visual search experiments, may require an ‘on-line’ system mediated by attention and parietal association regions.

Implications for current theories of object processing

Although the thesis was motivated by the ‘binding problem’, its findings are generally relevant to theories of visual processing. Of specific relevance are theories of object processing, where the role of colour is at the heart of the distinction between ‘edge-based’ and ‘surface-plus-edge’ theories (e.g., Biederman & Ju, 1987; Price & Humphreys, 1989). ‘Edge-based’ theories allocate a role for colour (and other surface information) only at a late stage of

processing once edges have been resolved. The present findings are not easily reconciled with a pure edge framework. It is difficult to conceive how automatic colour-shape integration (even to one's detriment, Chapter 4), occurring pre-attentively (Chapter 5, 6) and associated with early visual areas (Chapter 7), can be understood within an 'edge-based' framework. Rather this work supports a 'surface-plus-edge' account where diagnostic colour is an integral part of object processing (Price & Humphreys, 1989).

Directions for future research

Development of learned bindings

A direction for future research could examine how these learned bindings develop. From a developmental perspective, when do yellow and blue bananas become different and can we chart the neuronal substrate supporting this change? The same question may be addressed by trying to teach adults new conjunctions. For example associating red and circle. Is regular exposure enough to develop learned conjunctions? Do you need to attend to the conjunctions of elements for learning to take place? Can attending to one dimension be sufficient? Is attention to the item needed at all (e.g., is there learning of the conjunctive relation if conjunctions are repeatedly presented in the background and participants perform a task at fixation?

Rehabilitation

As discussed throughout this thesis many neurological disorders are associated with binding impairments. I have discussed feature integration deficits in visual neglect and extinction, but these difficulties are also central in Balint's syndrome and simultanagnosia. How can we remediate deficits in binding? Understanding binding, and particularly the development of

learned conjunctions, may be of clinical consequence for informing rehabilitation strategies. Outcomes from rehabilitation may also directly be an informative test of binding-theory.

fMR-adaptation

The development of fMR-adaptation methods allows us to begin addressing another aspect of the colour – form binding problem. Is neural coding sensitive only to whether particular colour-shape relations are categorically correct, but do the absolute values of colour and shape not matter? I have identified areas in the visual cortex sensitive to colour-shape binding, but are they sensitive to different correct colours? For example, we could compare blocks of correctly coloured stimuli (but different – i.e. red, green and yellow pepper) with blocks of the same object but incorrectly coloured. Would areas LOC/V4/, medial and anterior regions of the ventral stream (e.g. aCoS) show repetition suppression (i.e. a decrease in the BOLD response) when the varied colour is correct, but not so when the colour varied is incorrect? If there are separate conjunction units (i.e. one for a red pepper, one for a green pepper) then we would not expect repetition suppression to different chromatic depictions. By contrast, within the framework of a distributed cell assembly, the same shape would be associated with several colours and therefore we would expect repetition suppression.

Overall Conclusions

My thesis was motivated by a desire to explore how segregated visual information is integrated and our perception coherent and whole, which is known as the ‘binding problem’. I have succeeded in contributing to a future solution to this problem in the following ways. Firstly, I have deepened our understanding of pre-attentive grouping processes, which I have shown can affect temporal and spatial coding. Secondly, I have provided evidence for the crucial role of learning in overcoming attention limitations on the binding process, and proposed early visual areas as the neural correlate of these effects. This thesis alone doesn’t

solve the binding problem; rather, its most important contribution is to give rise to challenging new questions. Most pertinently here is our understanding of how learning may form part of the ‘binding’ solution.

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Appendix 1

Table 16: Proportion of omissions when items are identical (in both shape and colour) compared with when they were different (in both shape and colour).

	<i>Same</i>				<i>Different</i>			
	<i>Exp1</i>	<i>Exp2</i>	<i>Exp3</i>	<i>Exp4</i>	<i>Exp1</i>	<i>Exp2</i>	<i>Exp3</i>	<i>Exp4</i>
AS	0.80	0.43	0.71	0.56	0.65	0.60	0.83	0.82
HB	0.74	0.17	0.57	0.32	0.65	0.19	0.79	0.59
MC	0.79	0.84	0.53	0.57	0.51	0.61	0.78	0.61
MP	0.78	0.50	0.41	0.44	0.69	0.62	0.65	0.55

Table 17: Proportion of omissions when only the task relevant feature was repeated vs. not repeated.

	<u><i>Task Relevant Repeat</i></u>				<u><i>Task Relevant Non-Repeat</i></u>			
	<i>Exp1</i>	<i>Exp2</i>	<i>Exp3</i>	<i>Exp4</i>	<i>Exp1</i>	<i>Exp2</i>	<i>Exp3</i>	<i>Exp4</i>
AS	0.76	0.46	0.77	0.64	0.62	0.65	0.87	0.68
HB	0.71	0.68	0.65	0.29	0.59	0.80	0.73	0.40
MC	0.69	0.38	0.77	0.47	0.50	0.36	0.78	0.55
MP	0.74	0.54	0.50	0.49	0.68	0.46	0.46	0.66

Appendix 2

Object Name	Correct Colour	Incorrect Colour
<i>APPLE</i>	RED	PURPLE
<i>AUBERGINE</i>	PURPLE	GREEN
<i>AVOCADO</i>	GREEN	BLUE
<i>BANANA</i>	YELLOW	RED
<i>BLUEBERRY</i>	BLUE	GREEN
<i>BROCCOLI</i>	GREEN	RED
<i>BUTTERNUTSQUASH</i>	ORANGE/BROWN	GREEN
<i>CARROT</i>	ORANGE	GREEN
<i>CELERY</i>	GREEN	YELLOW
<i>CHERRY</i>	RED	YELLOW
<i>CORN</i>	YELLOW	GREEN
<i>COURGETTE</i>	GREEN	RED
<i>CUCUMBER</i>	GREEN	BROWN
<i>FENNEL</i>	GREEN/WHITE	ORANGE
<i>KIWI</i>	GREEN	PURPLE
<i>LEEK</i>	GREEN/WHITE	ORANGE
<i>LEMON</i>	YELLOW	RED
<i>LETTUCE</i>	GREEN	YELLOW
<i>MANGO</i>	GREEN	PURPLE
<i>MELON</i>	BROWN/YELLOW	RED
<i>NUT</i>	BROWN	GREEN
<i>PEAR</i>	YELLOW	RED
<i>PEAS</i>	GREEN	RED
<i>PEPPER</i>	RED	PURPLE
<i>PLUM</i>	PURPLE	YELLOW
<i>POTATO</i>	BROWN	GREEN
<i>PUMPKIN</i>	ORANGE	RED
<i>PURPLEGRAPES</i>	PURPLE	BROWN
<i>RASPBERRY</i>	RED	GREEN
<i>REDCABBAGE</i>	PURPLE	ORANGE
<i>REDCHILLI</i>	RED	PURPLE
<i>REDONION</i>	PURPLE	GREEN
<i>SPROUT</i>	GREEN	ORANGE
<i>STRAWBERRY</i>	RED	GREEN
<i>TOMATO</i>	RED	BROWN
<i>WATERMELON</i>	RED	GREEN

Appendix 3

Object Name	Correct Colour	Incorrect Colour
APPLE	RED	BLUE
APRICOT	ORANGE	BLUE
ASPARAGUS	GREEN	PURPLE
AUBERGINE	PURPLE	GREEN
AVOCADO	GREEN	PURPLE
BANANA	YELLOW	BLUE
BASIL	GREEN	PURPLE
BEETROOT	PURPLE	GREEN
BLUEBERRY	BLUE	YELLOW
BOKCHOY	GREEN	PURPLE
BROCCOLI	GREEN	PURPLE
BUTTERNUTSQUASH	ORANGE	BLUE
CARROT	ORANGE	BLUE
CAULIFLOWER	WHITE/GREEN	PURPLE
CELERY	GREEN	PURPLE
CHERRY	RED	GREEN
COCONUT	BROWN	GREEN
CORN	YELLOW	PURPLE
COURGETTE	GREEN	PURPLE
CUCUMBER	GREEN	PURPLE
FENNEL	WHITE/GREEN	PURPLE
FIG	PURPLE	GREEN
GARLIC	WHITE	BLUE
GINGER	YELLOW	BLUE
GREENCABBAGE	GREEN	PURPLE/BLUE
GREENCHILLI	GREEN	PURPLE
GREENGRAPES	GREEN	PURPLE
GREENPEPPER	GREEN	PURPLE
KALE	GREEN	PURPLE
KIWI	GREEN	PURPLE
LEAF	GREEN	PURPLE
LEEK	WHITE/GREEN	PURPLE
LEMON	YELLOW	BLUE
LETTUCE	GREEN	PURPLE
LIME	GREEN	PURPLE
LYCHEE	WHITE	BLUE
MANGO	GREEN	PURPLE/BLUE
MELON	YELLOW	BLUE
MUSHROOM	WHITE	BLUE
NECTARINE	ORANGE	BLUE
NUT	BROWN	BLUE
ONION	BROWN	BLUE
ORANGE	ORANGE	BLUE
PAPYA	GREEN/ORANGE	PURPLE/BLUE
PARSLEY	GREEN	PURPLE
PARSNIP	WHITE	BLUE
PEACH	ORANGE	BLUE
PEAR	YELLOW	BLUE
PEAS	GREEN	PURPLE
PHYSALIS	ORANGE	BLUE
PINEAPPLE	YELLOW/BROWN/GREEN	BLUE/PURPLE

<i>PINECONE</i>	BROWN	GREEN
<i>PLUM</i>	PURPLE	GREEN/BLUE
<i>POMEGRANATE</i>	RED	GREEN
<i>POTATO</i>	BROWN	BLUE
<i>PUMPKIN</i>	ORANGE	BLUE
<i>PURPLEGRAPES</i>	PURPLE	GREEN
<i>RADISH</i>	RED	GREEN
<i>RASPBERRY</i>	RED	GREEN
<i>REDCABBAGE</i>	PURPLE	GREEN/BLUE
<i>REDCHILLI</i>	RED	GREEN/BLUE
<i>REDONION</i>	PURPLE	GREEN
<i>REDPEPPER</i>	RED	GREEN/BLUE
<i>ROSEMARY</i>	GREEN	PURPLE
<i>SHARONFRUIT</i>	ORANGE	BLUE
<i>SPRINGONION</i>	GREEN	PURPLE
<i>SPROUT</i>	GREEN	PURPLE
<i>STRAWBERRY</i>	RED	GREEN
<i>SUGARSNAPPEA</i>	GREEN	PURPLE
<i>SWEDE</i>	WHITE/PURPLE	BLUE
<i>SWEETPOTATO</i>	ORANGE	BLUE
<i>TOMATO</i>	RED	GREEN
<i>WATERMELON</i>	RED	GREEN
<i>YELLOWPEPPER</i>	YELLOW	BLUE